SYSTEMATICS OF THE "SPINY SOLANUMS": MOLECULAR PHYLOGENETICS OF *SOLANUM* SECTION *ANDROCERAS*, SUBGENUS *LEPTOSTEMONUM,* AND A REVISION OF *SOLANUM* SECTION *ERIOPHYLLUM*

by

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STATEMENT OF DISSERTATION APPROVAL

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ABSTRACT

The heart of systematics lies in understanding the diversity of organisms, including the discovery, description, classification, and the relationships between them. Here, I examine the systematics of the plant genus *Solanum* (Solanaceae), specifically, species within the large Leptostemonum clade. The Leptostemonum clade contains ca. 350-450 species and is characterized by the presence of stellate hairs and epidermal prickles, leading to the common name of the "spiny solanums." Here, I present three studies within the spiny solanums. First, I present a molecular phylogenetic analysis of a group of ca. 12 species known as *Solanum* section *Androceras*. Many unusual morphological features, including zygomorphic flowers, dry fruits enveloped by a tightly accrescent calyx, and unique chemical compounds, characterize this group. I use molecular phylogenetic techniques to examine the monophyly of this group, clarify the relationship between section *Androceras* and closely related members of the spiny solanums, and resolve the relationships between species within the section. Second, I present a molecular phylogenetic analysis of the new world members of the Leptostemonum clade to circumscribe the major clades and examine the relationships between them. Specifically, I increase taxon sampling of many of the large groups underrepresented in previous studies, including sections and species that have not previously been sampled, to delimit 14 clades within the spiny solanums. Finally, I present a taxonomic revision of *Solanum* section *Eriophyllum*, a group of 12 viny species

native to the Neotropics. In this revision, I review the morphology, taxonomic history, nomenclature, ecology, distribution, reproductive biology, and phylogeny of the section. The results of these studies will help to increase our understanding of a large, economically important group of plants.

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CHAPTER 1

INTRODUCTION

One of the most basic questions in biology relates to the number of living organisms on earth. Although this question has been posed for centuries, we do not know to within an order of magnitude how many species there are on earth; current estimates of species diversity vary from under 5 million to over 50 million species (May 1988). Yet, despite this wide range of estimates, there are only roughly 6000 taxonomists working to classify all of earth's organisms (Wilson 2004).

The diversity of seed plants, a relatively well-studied group compared to other taxa, was traditionally placed around 250,000 species (Mabberley 1997). More recent accounts, particularly those utilizing the abundant online species lists and databases, have increased this number to around 350,000 (Paton et al. 2008) or even 400,000 (Govaerts 2001). To begin to understand the biology of life on earth, scientists must continue to collect, identify, and describe these organisms, as well as make their classifications accessible to others. A current wave of global biodiversity study comes at a time of great technological advances that give the ability to put taxonomic work into a phylogenetic context. The phylogenetic perspective can be used to assess character evolution, helping scientists understand adaptation and diversification.

Solanum (Solanaceae) is one of the 10 largest genera of flowering plants and is thought to contain approximately 1500 species (Frodin 2004; Bohs 2005). The size of this

"giant genus" makes it difficult for a single researcher to study the whole, or even a large part of it. However, the size and diversity of the genus also gives unprecedented opportunities for morphological, biogeographical, and molecular studies (Weese and Bohs 2007). *Solanum* has a pantropical distribution with a center of diversity in the New World tropics. Species exhibit a variety of habits, including herbs, vines, lianas, shrubs, and small trees. Additionally, *Solanum* has an incredible economic importance as it includes species such as the tomato (*S. lycopersicum* L.), eggplant (*S. melongena* L.), and potato (*S. tuberosum* L.). While these particular cultivated species have been intensively studied, little is known about many of the other species in the genus.

Solanum has been the focal point of recent studies ranging from sequencing the genome of the tomato (http://www.sgn.cornell.edu/, Mueller et al. 2005) to species level taxonomy (PBI *Solanum* Project, www.solanaceaesource.org) Analyses of DNA sequence data have aided in resolving the relationships throughout the Solanaceae and have helped to identify the major clades within *Solanum* (Bohs 2005; Levin et al. 2006; Weese & Bohs 2007). These phylogenies now serve as a framework to evaluate current sectional circumscriptions and identify groups that are in need of revisionary work.

The largest monophyletic group recognized by Weese and Bohs (2007) within *Solanum* is the Leptostemonum clade. With ca. 350-450 species, this clade contains almost one third of the genus and has been recognized since at least the time of Linnaeus (1753) due to the presence of epidermal prickles. These prickles have given rise to the common name of the "spiny solanums" (Levin et al. 2006). The goal of my dissertation is to increase understanding of the taxonomy and phylogenetic relationships within the spiny solanums. The studies presented here are 1) a molecular phylogenetic study of

section *Androceras,* 2) a phylogenetic study of the new world spiny solanums, and 3) a taxonomic revision of section *Eriophyllum*, a section formerly known as section *Micracantha*.

Solanum section *Androceras* is a group of approximately 12 species of weedy herbs or perennials from a persistent woody roots that range from the midwestern U.S.A. through Mexico to Honduras. They are unusual in the spiny solanums in having bilaterally symmetrical flowers with four small, straight upper anthers and an elongate lower anther. Additionally, the fruits of section *Androceras* are not fleshy berries as is typical of the spiny solanums but instead are dry at maturity and tightly enveloped by a prickly, accrescent calyx. The section was taxonomically revised by Whalen (1979) but to date, there have been limited molecular phylogenetic studies of the section. In Chapter 2, we use molecular phylogenetic techniques to investigate the monophyly of section *Androceras*, examine the phylogenetic relationships of the section with closely related members of the Leptostemonum clade, test the monophyly of Whalen's (1979) series and species, and examine selected species-level relationships to test hypotheses of character evolution and speciation.

While section *Androceras* has morphological synapomorphies that make it relatively distinct, other groups within the Leptostemonum clade are more difficult to define. In Chapter 3, we present a phylogenetic analysis that circumscribes the major clades within the New World species of spiny solanums and examines the relationships among them. This study builds on work by Levin et al. (2006) but increases taxon sampling for many of the large groups that were poorly sampled in that study, including sections that have not previously been sampled, and clarifies clade limits and species

composition of these groups. Our study delimits 14 clades, including the newly designated Asterophorum, Gardneri, Sisymbriifolium, and Thomasiifolium clades. Finally, we establish the placement of species not previously sampled, especially those endemic to Brazil. The results of this study give an increased understanding of the evolution of the Leptostemonum clade by defining monophyletic groups within it and identify areas of the phylogenetic tree that remain unresolved and require further sampling.

The delimitation of monophyletic groups from our large-scale molecular phylogenetic study is instrumental for taxonomic revision of groups within the spiny solanums. One such group is section *Eriophyllum*. Whalen (1984) recognized 11 species in this group of Neotopical vines while Nee (1999) placed 18 species in his section *Micracantha*. Both Whalen (1984) and Nee (1999) used only morphological characters to define this group, especially focusing on the fact that it contains plants that climb via recurved prickles. Whalen noted that the section was in serious need of taxonomic revision, but it has yet to receive a complete revision. Chapter 4 is a taxonomic revision of these species. We recognize the group as section *Eriophyllum* because *S. micracanthos* (a synonym for *S. subinerme*) was shown by Stern et al. (in press) to belong to the Torva clade and *S. jamaicense*, a member of the group of interest, was chosen by D'Arcy (1972) as the lectotype for section *Eriophyllum*. In this revision, we review the morphology, taxonomic history, nomenclature, ecology, distribution, reproductive biology, and phylogeny of *Solanum* section *Eriophyllum*.

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CHAPTER 2

PHYLOGENETIC RELATIONSHIPS IN *SOLANUM* SECTION *ANDROCERAS* (SOLANACEAE)

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Phylogenetic Relationships in *Solanum* Section *Androceras* (Solanaceae)

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Abstract—The Leptostemonum clade of *Solanum* contains approximately 350–450 species, including the cultivated eggplant, *S. melongena*. This clade is characterized by the presence of prickles and apically attenuate anthers. *Solanum* section *Androceras*, the focus of this study, is a group of ca. 12 species belonging to the Leptostemonum clade. This section is unusual in the genus because of its mostly north temperate distribution and distinctive zygomorphic, heterantherous, and enantiostylous flowers. We infer phylogenetic relationships among 43 *Solanum* taxa, including 11 species and all varieties of sect. *Androceras*, using DNA sequence data from two nuclear regions (ITS and the granule-bound starch synthase gene [GBSSI or *waxy*]) and the chloroplast region *trnT-F*. The combined phylogenetic tree supports sect. *Androceras* as a monophyletic group sister to *Solanum* sect. *Crinitum*. Only one of the three series proposed by previous taxonomists, ser. *Pacificum*, is supported as monophyletic. *Solanum tenuipes* from the northern Chihuahua Desert is sister to the remaining species in sect. *Androceras*. Species-level relationships were also examined and it was found that two species, *S. heterodoxum* and *S. citrullifolium*, are not monophyletic. The ancestral flower color in sect. *Androceras* appears to be violet, with white and yellow flowers restricted to more derived clades. Characters formerly used to diagnose ser. *Androceras*, such as exclusively branched hairs and lack of complex foliar flavonoids, appear to have evolved more than once in the section.

Keywords—enantiostyly, heteranthery, ITS, Mexico, *trnT-F*, *waxy*.

Solanum L. (Solanaceae), thought to contain approximately 1,400 species, is one of the 10 largest genera of flowering plants (Frodin 2004; Bohs 2005). It also contains economically important species such as the tomato (*S. lycopersicum* L.), eggplant (*S. melongena* L.), and potato (*S. tuberosum* L.). Recent studies of the genus range from sequencing the genome of the tomato (Mueller et al. 2005; http://www.sgn.cornell.edu/) to resolving phylogenetic relationships within *Solanum* as well as species level taxonomy (Knapp et al. 2004; http://www.nhm.ac.uk/solanaceaesource/). With respect to the phylogeny of the genus, analyses of DNA sequence data have helped to identify the major groups within *Solanum*, the largest of which is the Leptostemonum clade with approximately 350–450 species (Bohs 2005; Levin et al. 2006). This group is commonly known as the "spiny solanums" due to the presence of sharp epidermal prickles.

Within the Leptostemonum clade, *Solanum* sect. *Androceras* is unique in many features including distribution, flower and fruit morphology, and chemistry. Its morphological characteristics, specifically floral morphology, are so distinct that Nuttall (1818) placed the species in the genus *Androcera* Nutt., although he noted the similarities between *Androcera* and *Solanum*. Marzell (1927) placed the species of *Androcera* into *Solanum* sect. *Androceras*. Whalen (1979a) provided a detailed revision of *Solanum* sect. *Androceras*, including 12 species and 10 varieties, and divided the section into three series (discussed below; Table 1) based on hair, flower, seed, and chemical characteristics as well as geographical distributions. Species in the section range from the midwestern U. S. A. through Mexico to Honduras, with the highlands around Mexico City, the northern Chihuahuan Desert, and the west coast of Mexico as centers of diversity (Table 1). This section is one of the only groups in *Solanum* to have a primarily north temperate distribution. Within its range, species of sect. *Androceras* are weedy annual herbs or perennials from persistent woody roots. Many species grow in warm, semiarid to arid regions with unpredictable seasonal rainfall. Chromosome counts have been reported for all species in sect. *Androceras*, and all are diploids with $2n = 24$ (Whalen 1979a).

Typical *Solanum* flowers are radially symmetrical with stamens dehiscing by terminal pores. They are usually buzz pollinated, ejecting pollen from the pores when vibrated by bees. Species in sect. *Androceras* conform to this basic plan, but are further specialized in being bilaterally symmetrical. The stamens within a single flower are unequal in size, with four small, straight upper anthers and an elongate lower anther (heteranthery; Bohs et al. 2007). This elongated, inwardly-curved lowermost stamen can be a different color than the other stamens and is opposed by a slender style of similar shape (Fig. 1a, b, c). The position of the style alternates between the right and left side of the flower along the inflorescence, resulting in "mirror-image" flowers (enantiostyly).

Flowers of sect. *Androceras*, specifically *S. rostratum*, have been extensively observed in field and natural history studies with a focus on the unusual stamen dimorphism (Todd 1882; Harris and Kuchs 1902; Bowers 1975; Jesson and Barrett 2002). The upper four small stamens provide the pollen that the bees use for food, whereas the lowermost, elongated stamen acts as a pollinating stamen by depositing pollen on one side of the bee's abdomen where it cannot efficiently be removed (Bowers 1975; Vallejo-Marin et al. 2009). The alternating right- and left-handed flowers have been shown to have higher outcrossing rates than plants manipulated to have either straight styles or right-handed or left-handed flowers only (Jesson and Barrett 2002). This might be especially important in maintaining genetic diversity in sect. *Androceras*, where all tested species have been found to be self-compatible (Whalen 1979a).

Most species of *Solanum* have fleshy berries, whereas fruits in sect. *Androceras* are dry at maturity and tightly enveloped by a prickly, accrescent calyx (Fig. 1d). Whalen (1979a) showed that these represent a "censer" dispersal mechanism, also seen in other members of the Leptostemonum clade, particularly those of dry habitats, in which the fruits remain on the plant and the calyx splits open, tearing the dry berry (Symon 1984; Knapp 2002). This then acts like a "censer," shaking loose the small seeds. The large number of seeds produced by a single plant, in some cases over 5,000 seeds from an individual, corresponds to the observation that *Solanum* sect. *Androceras* is typically a weedy, colonizing group of species.

Some species of sect. *Androceras* have a unique suite of flavonoid compounds, such as 8-hydroxyflavonoids and C-glycosylflavones, not found in other *Solanum* groups (Whalen 1978a). Differences also exist in the chemical profiles between the three series within the section recognized

TABLE 1. Species of *Solanum* sect. *Androceras*, including the series and their distributions according to Whalen (1979a). All taxa except *S. leucandrum* were sampled in this study.

Solanum section *Androceras* (Nutt.) Marzell	Geographic Distributions
Series *Androceras*	
S. angustifolium Mill.	Tropical Mexico south to Honduras
S. fructo-tecto Cav.	Distrito Federal, Hidalgo, and México States with collections from Ciudad Durango and the Sierra Madre, Mexico
S. johnstonii Whalen	Endemic to eastern Durango State, Mexico
S. rostratum Dunal	Widespread from Mexico City through the Great Plains, U.S.A.; introduced worldwide
S. tribulosum Schauer	Querétaro to southeastern Puebla State, Mexico
Series *Pacificum* Whalen	
S. grayi Rose var. *grayi*	Southern Sonora and northern Sinaloa, Mexico
var. *grandiflorum* Whalen	Southern Sinaloa and south along the Sierra Madre, east to Guerrero inland in central Mexico to Morelos
S. leucandrum Whalen	Known only from the type locality in western Puebla, Mexico
S. lumholtzianum Bartlett	Southern Arizona, and Sonora to northern Sinaloa, Mexico
Series *Violaceiflorum* Whalen	
S. citrullifolium A. Braun var. *citrullifolium*	North-central Coahuila, Mexico to the Davis Mts. of western Texas, with a cluster of populations in central Texas
var. *knoblochii* Whalen	Known only from two localities in Tarahumara country of western Chihuahua, Mexico
var. *setigerum* Bartlett	Eastern Chihuahua and western Coahuila, occasionally Presidio County, Texas
S. davisense Whalen	Davis, Chinati, and Chisos Mts. of west Texas and Sierra del Carmen in northern Coahuila, Mexico
S. heterodoxum Dunal var. *heterodoxum*	Veracruz northwest across Puebla and Hidalgo to San Luis Potosí, Mexico
var. *novomexicanum* Bartlett	Mountains of north-central New Mexico
var. *setigeroides* Whalen	Northern Chihuahua, southeastern Arizona, and southwestern New Mexico
S. tenuipes Bartlett var. *tenuipes*	Eastern Coahuila State, Mexico to Brewster, Terrel, Val Verde, and Maverick Counties, Texas
var. *latisectum* Whalen	Presidio County, Texas south along the Chihuahua and Coahuila borders to eastern Durango, Mexico

by Whalen (1979a), such as the presence of methoxylated aglycones, 8-hydroxyflavonoids and various flavones in sers. *Violaceiflorum* and *Pacificum* that are absent in ser. *Androceras*. The major chemical differences between sers. *Violaceiflorum* and *Pacificum* are flavones with chrysoeriol type B-rings in ser. *Pacificum* and the presence of 8-oxygenated flavonols in ser. *Violaceiflorum* (Whalen 1978a).

Although Whalen (1979a) revised sect. *Androceras* and included a cladistic analysis based on 14 morphological and chemical traits, to date there have been limited molecular phylogenetic studies of this section. Two species of sect. *Androceras*, *S. rostratum* and *S. citrullifolium*, were included in molecular phylogenies of the entire Leptostemonum clade and were strongly supported as sister taxa (Levin et al. 2006; Bohs et al. 2007). These studies place sect. *Androceras* sister to sect. *Crinitum* Child with moderate support (84% bootstrap and 1.0 posterior probability in Levin et al. 2006). This relationship had not previously been proposed due to the fact that sect. *Crinitum* is a South American group of large shrubs and trees with fruits that may reach 10 cm in diameter and large flowers that are not heterantherous. A close relationship between sect. *Androceras* and *S. sisymbriifolium* of sect. *Cryptocarpum* Dunal has been proposed in the past due to their similar leaves, inflorescences, and accrescent calyces (Dunal 1813, 1852; Walpers 1844; Danert 1970; Whalen 1979a; Lester et al. 1999). Both Weese and Bohs (2007) and Bohs et al. (2007) have found that *S. sisymbriifolium* is sister to a clade composed of sect. *Androceras* and sect. *Crinitum*. Whalen (1979a) favored sect. *Nycterium* (Venten.) Walp. as the sister group to sect. *Androceras* based on morphological similarities, but molecular studies unequivocally place the members of sect. *Nycterium* quite distant from sect. *Androceras* (Levin et al. 2006; Bohs et al. 2007; Weese and Bohs 2007). While these studies provide hypotheses about relationships between sect. *Androceras* and other *Solanum* sections, they did not extensively sample from within the section.

In this paper we use molecular phylogenetic methods to 1) test the monophyly of sect. *Androceras* as currently circumscribed, 2) examine the phylogenetic relationships of sect. *Androceras* with closely related members of the Leptostemonum clade, 3) test the monophyly of Whalen's (1979a) series and species within sect. *Androceras*, and 4) examine selected species-level relationships to test hypotheses of character evolution and speciation proposed by Whalen (1979a).

MATERIALS AND METHODS

Taxon Sampling—Eleven of the 12 species and all 10 varieties in sect. *Androceras* sensu Whalen (1979a) were sampled for this study (Table 1). We were unable to obtain high quality genomic DNA for *Solanum leucandrum*, which is known only from the type locality in Puebla, Mexico, due to a lack of available herbarium material. Specimens were determined using keys found in Whalen (1979a), with almost half of the specimens determined by the late Michael D. Whalen himself (indicated with asterisks in Appendix 1). We also included six members of sect. *Crinitum* as well as *S. sisymbriifolium*, both shown by previous molecular studies to be closely related to sect. *Androceras* (Levin et al. 2006; Bohs et al. 2007). Five other more distantly related species from the Acanthophora and Bahamense clades of the Leptostemonum clade were included to ensure sufficient outgroup sampling, and the tree was rooted using *S. betaceum*, an even more distantly related *Solanum* from outside the Leptostemonum clade. The final data set included 43 accessions, representing 11 named species of sect. *Androceras* as well as 12 outgroup species. All taxa, along with voucher information and GenBank accession numbers, are listed in Appendix 1.

DNA Extraction, Amplification, and Sequencing—Total genomic DNA was extracted from fresh, silica gel-dried, or herbarium material using the DNeasy plant mini extraction kit (Qiagen, Inc., Valencia, California). Amplification for each gene region followed standard procedures described in Taberlet et al. (1991), Bohs and Olmstead (2001), and Bohs (2004) for the *trnT-L* and *trnL-F* intergeneric spacer regions; Levin et al. (2005) for *waxy*; and Levin et al. (2006) for ITS. The ITS region was amplified as a single fragment using primers ITSleu1 (Bohs and Olmstead 2001) and ITS4 (White et al. 1990) using PCR conditions described in Bohs and Olmstead (2001). When possible, *trnT-F* and *waxy* were amplified as single fragments using primers a and f for *trnT-F* (Taberlet et al. 1991) and primers waxyF and waxy2R for *waxy* (Levin et al. 2005). Amplification conditions for *trnT-F* followed Bohs and Olmstead (2001); conditions for *waxy* followed Levin et al. (2005). When necessary, overlapping fragments were amplified and assembled, using primers a with d, and c with f to amplify *trnT-F*, and primers waxyF with 1171R, and 1058F with 2R to amplify *waxy*. Specimens not amplifying for *waxy* were amplified in

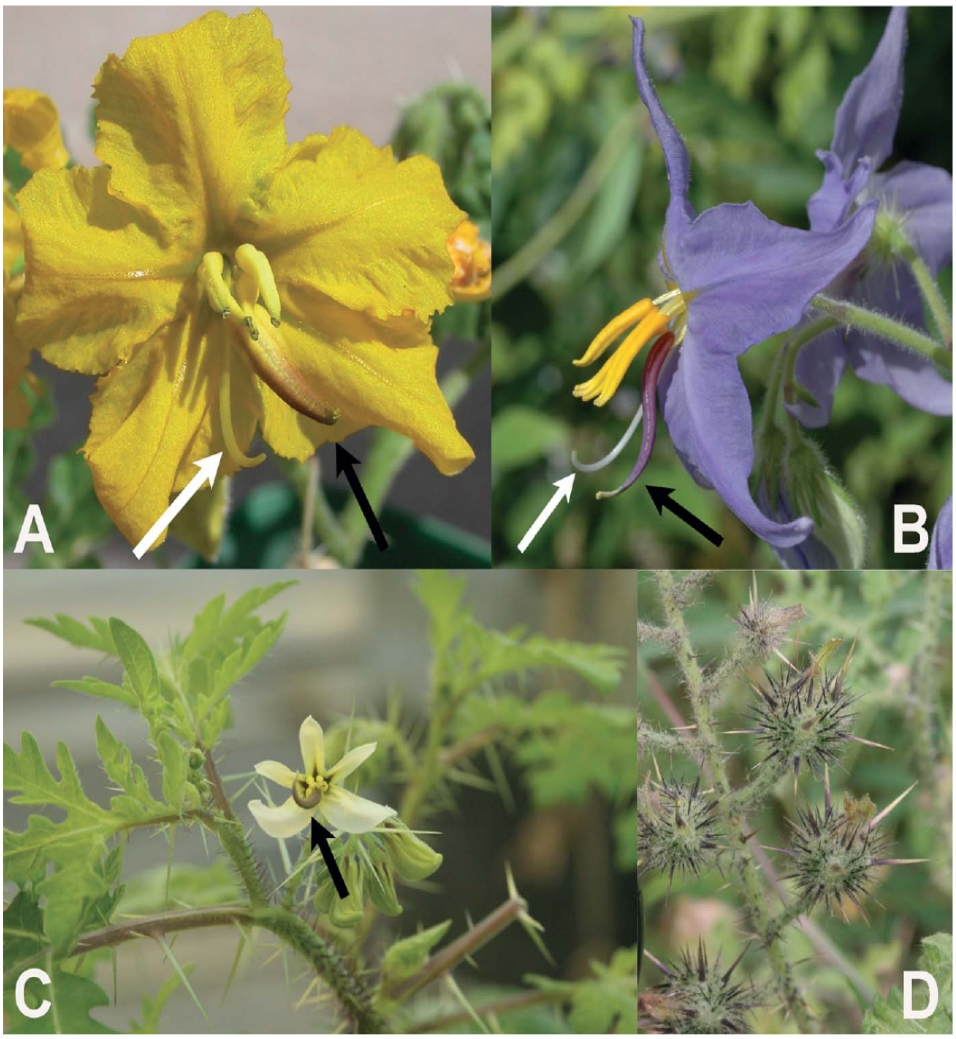

FIG. 1. Representatives of *Solanum* sect. *Androceras*. White arrows indicate the style and black arrows indicate the enlarged lower anther. A. *S. rostratum* of Whalen's ser. *Androceras* and our Rostratum clade. B. *S. citrullifolium* var. *citrullifolium* of Whalen's ser. *Violaceiflorum* and our Setigeroid clade. C. *S. grayii* var. *grandiflorum* of Whalen's ser. *Pacificum* and our Pacificum clade. D. Typical fruits of sect. *Androceras* from *S. rostratum*. Photos C, D courtesy of M. Vallejo-Marín.

even smaller fragments using primers waxyF and the newly developed EX4R (5′-CACAACCTGAACCTAAG-3′) for the first fragment, the new primer EX4F (5′-CTATGGCCCCAAAGCTGGAC-3′) and 1171R for the second fragment, primers 1058F and 3′N (Peralta and Spooner 2001) for the third fragment, and primers 3′F (Miller et al. 1999) and 2R for the final fragment.

Amplification products were cleaned using the Promega Wizard SV PCR Clean-Up System (Promega Corporation, Madison, Wisconsin). The University of Utah DNA Sequencing Core Facility performed sequencing on an ABI automated sequencer. Sequences were edited in Sequencher (Gene Codes Corp., Ann Arbor, Michigan) and all new sequences were submitted to GenBank.

Morphological Data—The data matrix presented in Whalen (1979a; Table 6), representing 11 morphological, two chemical, and one isozyme character for species in sect. *Androceras* was added to the combined molecular data matrix with characters for outgroup species coded as missing data.

Sequence Alignment and Analysis—Sequence alignment for all gene regions was straightforward and performed visually using Se-Al (Rambaut 1996). The aligned datasets and representative phylogenetic trees are available in TreeBASE (study number S2642).

Parsimony Analyses—Maximum parsimony (MP) analyses were performed on each dataset separately and on the combined dataset both with and without morphological data using PAUP*4.0b10 (Swofford 2002). All characters were weighted equally in analyses that implemented tree bisection reconnection (TBR) branch swapping with 1,000 heuristic random addition replicates, each limited to 1,000,000 swaps per replicate. Gaps were treated as missing data. Bootstrapping (BS; Felsenstein 1985) was used to evaluate branch support with 1,000 random addition replicates and TBR branch swapping limited to 1,000,000 swaps per replicate. Datasets were further analyzed using TNT (Goloboff et al. 2008) to search for shorter trees than were obtained in standard PAUP analyses. Congruence of the datasets was tested using partition homogeneity tests (incongruence length difference test [ILD]; Farris et al. 1994, 1995)

implemented in PAUP*. One thousand heuristic partition homogeneity replicates were completed, each with 10 random addition sequence replicates, TBR branch-swapping, MulTrees off, and gaps treated as missing data.

Bayesian Analyses—Prior to Bayesian analyses (BI), a general model of nucleotide evolution was selected for each of the separate and combined datasets using the AIC criterion identified in Modeltest 3.7 (Posada and Crandall 1998). MrBayes 3.1 (Huelsenbeck and Ronquist 2001) was used to analyze the individual and combined datasets. For each analysis 20 replicates were run of four Markov chains, each initiated from a random tree and sampled every 1,000 generations using the stop rule to stop the analysis when standard deviations between the runs reached 0.01. All parameters from each analysis were visualized graphically and the samples obtained prior to achieving stationarity were discarded as a burn-in.

Constraint Analyses—Constraint trees were constructed in MacClade 4 (Maddison and Maddison 2000) to constrain 1) each of Whalen's (1979a) series as monophyletic, 2) only the taxa in ser. *Androceras* as monophyletic, 3) only the taxa in ser. *Violaceiflorum* as monophyletic, and 4) the yellow-flowered taxa as monophyletic. Parsimony analyses were performed with the constraint enforced using TBR branch swapping with 1,000 heuristic random addition replicates, each limited to 1,000,000 swaps per replicate. These trees were then compared with the most parsimonious trees using the Templeton test (Templeton 1983; Prager and Wilson 1988).

Results

Phylogenetic Analyses—Descriptive statistics for the molecular datasets and phylogenetic analyses for the 43 accessions are given in Table 2. Missing data comprised 0.00087% of the combined data matrix (149 bases from a total of 171,907). For the individual datasets, the *trnT-F* region yielded the least resolved phylogeny in both MP and BI analyses. The *waxy* data produced the most resolved trees with the highest number of strongly supported ingroup nodes (Table 2). In general, the parsimony strict consensus and BI majority rule consensus trees from the combined dataset differed only in the degree of resolution, with BI tree topologies more resolved than parsimony trees (Table 2). Clades with low posterior probabilities (PP) in BI analyses were often collapsed in MP strict consensus trees (individual trees not shown).

More nodes were strongly supported by combining the three datasets than were obtained in any of the separate analyses (Table 2; Fig. 2). Inclusion of morphological data did not affect either the topology or resolution of the phylogeny compared to the combined molecular dataset analyzed alone. The only differences between these and the strictly molecular trees were slight differences in support values for a few nodes.

Topological Conflicts—According to the results of the ILD tests, the three data partitions in the combined data set were found to be incongruent ($p = 0.033$), so pairwise ILD tests were run. The nuclear datasets (ITS and *waxy*) were found to be incongruent ($p = 0.01$) as were the *waxy* and *trnT-F* datasets ($p = 0.01$). The only congruent datasets were ITS and *trnT-F* ($p = 0.071$). The incongruence of the datasets is likely due to the disparity in the size and substitution rates of the different datasets (Dolphin et al. 2000; Barker and Lutzoni 2002; Darlu and Lecointre 2002). However, with few exceptions, each DNA sequence region consistently identified the same major, well-supported clades comprising identical species groups, but relationships among clades were often not strongly supported (BS values < 90%), or were unresolved, and thus cannot be considered conflicting under Wiens' (1998) criteria. The BI analysis gave more conflicting nodes (cutoff at < 0.95 PP), but posterior probabilities are known to be inflated relative to bootstrap values (Cummings et al. 2003; Erixon et al. 2003; Simmons et al. 2004). Our discussion will be focused on the topology of the BI majority rule and MP strict consensus trees based on combined molecular data (Fig. 2).

Phylogenetic Relationships—Sectional Relationships and Monophyly of Section *Androceras*—All data sets strongly support the monophyly of sect. *Androceras* as circumscribed by Whalen (1979a, 1984; 100% BS, 1.0 PP in ITS, *waxy* and combined gene trees and 99% BS, 1.0 PP in *trnT-F*).

Although not supported in the single-gene analyses, the combined dataset supports sect. *Crinitum* as sister to sect. *Androceras* (88% BS, 1.0 PP), with *Solanum sisymbriifolium* sister to the clade composed of sects. *Androceras* and *Crinitum* (85% BS, 1.0 PP).

Monophyly of the Series Within Section *Androceras*—Of the three series identified by Whalen (1979a), our phylogeny supports only ser. *Pacificum* as a monophyletic group, termed the Pacificum clade in Fig. 2. This relationship is supported in the individual ITS (87% BS, 1.0 PP) and *waxy* datasets (98% BS, 1.0 PP) but not in the *trnT-F* dataset; the combined dataset resolves this group with 100% BS and 1.0 PP. Three of the five species of ser. *Androceras* form a moderately to strongly supported Rostratum clade composed of *S. rostratum*, *S. fructotecto*, and *S. angustifolium* in the *waxy* only (82% BS, 1.0 PP) and combined trees (94% BS, 1.0 PP). *Solanum johnstonii* of ser. *Androceras* is unplaced in the ITS, *trnT-F*, and combined analyses; the *waxy* only analysis places this species as sister to the Pacificum clade with moderate support (86% BS, 1.0 PP). The final member of Whalen's ser. *Androceras*, *S. tribulosum*, is moderately supported (82% BS, 1.0 PP) as sister to a large clade of species, placed by Whalen (1979a) in ser. *Violaceiflorum*, in the combined analyses, but this relationship is not recovered in any of the individual analyses. Whalen's ser. *Violaceiflorum* is clearly polyphyletic, with a large clade composed of *S. heterodoxum* var. *setigeroides*, *S. citrullifolium* vars. *citrullifolium* and *setigerum*, and *S. davisense* forming a monophyletic group, here termed the Setigeroid clade, in the *waxy* only (99% BS, 1.0 PP) and combined analyses (92% BS, 1.0 PP; Fig. 2). The remainder of the taxa belonging to Whalen's ser. *Violaceiflorum*, including *S. tenuipes*, *S. citrullifolium* var. *knoblichii*, and *S. heterodoxum* vars. *heterodoxum* and *novomexicanum* form a grade at the base of the Androceras clade in the combined analyses. "Elder 46", a potentially undescribed

Table 2. Descriptive statistics for the datasets analyzed. Strongly supported nodes for parsimony indicate those with ≥ 90% BS; Bayesian strongly supported nodes are those with ≥ 0.95 PP.

Data Partition	Aligned Sequence Length	Number of Parsimony Informative Characters	Number of MP Trees	Tree Length	CI	RI	Number of Strongly Supported Nodes Parsimony (ingroup nodes)	Model Selected	Number of Strongly Supported Nodes Bayesian (ingroup nodes)
ITS	666	121	13,691	431	0.608	0.783	11 (6)	GTR + I + G	21 (15)
waxy	1,731	165	48	428	0.844	0.895	17 (12)	GTR + G	32 (24)
trnT-F	2,088	65	52,750	188	0.910	0.895	6 (3)	GTR + I + G	13 (8)
Combined	4,485	340	10	1,085	0.733	0.829	18 (12)	GTR	36 (24)
Combined + Morphological	4,499	354	6	1,127	0.726	0.828	16 (12)	GTR	38 (27)

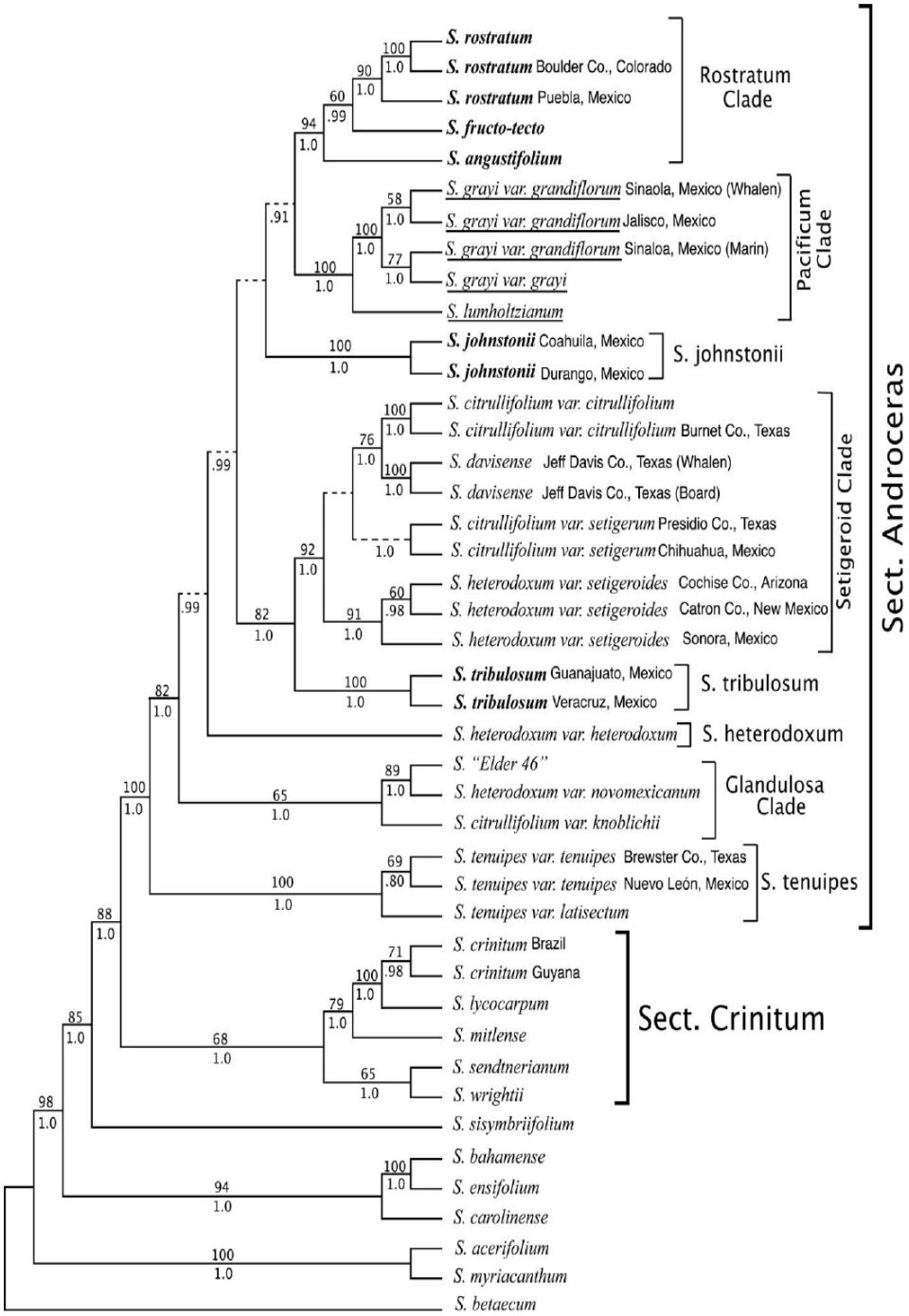

FIG. 2. 50% majority rule tree from the Bayesian analysis of the combined dataset. Numbers above branches are bootstrap values over 50%; numbers below branches are posterior probabilities from Bayesian analysis. Branches that collapse in the parsimony strict consensus tree but are present in the Bayesian majority rule tree are shown as dashed lines. Species of sect. *Androceras* placed by Whalen (1979a) in ser. *Androceras* are in bold italics, in ser. *Pacificum* are underlined, and in ser. *Violaceiflorum* are in nonbold italics. *Solanum* "Elder 46" was not placed in any of Whalen's (1979a) series; see text for discussion. The clades discussed in the text are labeled.

species, is strongly supported as sister to *S. heterodoxum* var. *novomexicanum* in the ITS only (85% BS, 0.98 PP), *waxy* only (87% BS, 1.0 PP) and combined analyses (89% BS, 1.0 PP), and, along with *S. citrullifolium* var. *knoblichii*, comprises a monophyletic group in the *waxy* only (100% BS, 1.0 PP) and combined analyses (65% BS, 1.0 PP), here termed the Glandulosa clade.

Species- and Infraspecific-Level Monophyly—Species-level monophyly was examined in a number of taxa with multiple accessions sequenced in the phylogeny. In the cases of *S. rostratum*, *S. grayi*, *S. johnstonii*, *S. davisense*, *S. tribulosum*, and *S. tenuipes*, all accessions of the same species formed monophyletic groups with strong support in the combined trees. Furthermore, the multiple accessions sequenced of *S. citrullifolium* var. *citrullifolium* and *S. heterodoxum* var. *setigeroides* each emerged as monophyletic in all combined analyses, but *S. citrullifolium* var. *setigerum* is paraphyletic in the combined MP strict consensus tree. However, *S. citrullifolium*, *S. heterodoxum*, and *S. grayi* var. *grandiflorum* were not supported as monophyletic, as multiple accessions of these taxa did not group together in the combined analyses.

Constraint Analyses—Constraining all of Whalen's series to be monophyletic resulted in trees significantly different than the most parsimonious tree from the combined dataset (Templeton's test $p = 0.0001$). When constraining sers. *Androceras* and *Violaceifolium* individually, the trees were also significantly different than the most parsimonious tree from the combined dataset ($p = 0.0455$ and 0.0477, respectively). Trees constraining all of the yellow-flowered taxa (i.e. species of ser. *Androceras* minus *S. tribulosum*) to monophyly were not significantly different than nonconstrained trees (Templeton's test $p = 0.6698$).

Discussion

Sectional Relationships and Monophyly of Section Androceras—Despite the various hypotheses regarding the sister group to sect. *Androceras*, our data support previous molecular studies in finding sect. *Crinitum* as sister to sect. *Androceras* (Levin et al. 2006; Weese and Bohs 2007). These groups are morphologically distinctive and this relationship merits further study. *Solanum sisymbriifolium* is sister to a clade composed of sect. *Androceras* and sect. *Crinitum* despite the fact that *S. sisymbriifolium* and sect. *Androceras* share highly divided leaves and strongly accrescent calyces, characters not found in sect. *Crinitum*. Lester et al. (1999) also found the seeds of sects. *Androceras* and *Cryptocarpum*, to which *S. sisymbriifolium* belongs, to be remarkably similar. We were not able to sample other members of sect. *Cryptocarpum* but further sampling might possibly place this group sister to sect. *Androceras*.

All three data sets strongly support the monophyly of sect. *Androceras* as circumscribed by Whalen (1979a, 1984). This molecular evidence, combined with unique morphological traits found in the leaves, flowers, and fruits, its distinctive flavonoid chemistry, and geographical distribution, leave little doubt that *Solanum* sect. *Androceras* is a monophyletic group.

Character Evolution and Monophyly of Whalen's Series in sect. Androceras—Whalen's (1979a) three series within sect. *Androceras* were distinguished by trichome, flower, and seed morphology as well as flavonoid chemistry and geographical distribution (Table 1). Whalen (1979a) circumscribed these series as natural phyletic groups; however, they were not defined in strict monophyletic terms (see paraphyly of sers. *Androceras* and *Violaceiflorum* in Fig. 15 in Whalen 1979a). It is clear in examining his matrix of morphological characters (Table 6 and Fig. 15 in Whalen 1979a), that many are homoplasious or autapomorphic. Additionally, the assessment of ancestral and derived characters as well as coding of characters are based on the author's interpretations (see secondarily lost characters in Table 5 in Whalen 1979a) and could be differently interpreted by other taxonomists. Given this and the fact that our combined molecular dataset contains 340 parsimony informative characters, it is not surprising that the addition of the 14 characters from Whalen's (1979a) dataset does not change the topology or resolution of the phylogeny (results not shown). The few synapomorphic characters in Whalen's (1979a) character matrix show support for ser. *Pacificum*, the only one of the three series that emerges as a monophyletic group in our molecular trees. Characters unique to this series include white, deeply stellate corollas, radially wrinkled seeds, and a geographical center of distribution on the Pacific slope of the Sierra Madre Occidental on the west coast of Mexico. Apparently these characters arose once in the Pacificum clade, although confirmation of this awaits sampling of the third member of ser. *Pacificum*, *S. leucandrum*.

Neither ser. *Androceras* nor *Violaceifolium* is supported as monophyletic in the molecular analyses. These series were paraphyletic in Whalen's (1979a) cladistic analysis and the nonmolecular characters that supported these groups are likely convergent. For instance, ser. *Androceras* was characterized by Whalen (1979a) as having stellate or multangulate cauline hairs and yellow corollas, lacking flavonoid compounds found in the other two series, and a distribution centered in the central Mexican highlands around Mexico City. These characters are found in species of the Rostratum clade (Fig. 2), but also in *S. johnstonii*, which does not form a part of this clade. Conversely, Whalen (1979a) placed *S. tribulosum* into ser. *Androceras* despite its pale blue or white corollas. Support and resolution along the backbone of the tree obtained here is weak or lacking, precluding firm conclusions about character evolution in sect. *Androceras* based on the most parsimonious trees. However, constraining all three series each to be monophyletic as well as constraining the taxa of Whalen's sers. *Androceras* and *Violaceifolium* individually to be monophyletic resulted in trees significantly different than the most parsimonious trees from the combined dataset. This further indicates that these two series are likely nonmonophyletic and that the characters that Whalen proposed to diagnose them have evolved multiple times. On the other hand, when all yellow-flowered taxa (i.e. species of ser. *Androceras* minus *S. tribulosum*) were constrained to monophyly, the constrained trees were not significantly different than nonconstrained trees. Therefore, the hypothesis of a single origin of yellow corollas within sect. *Androceras* cannot be rejected.

According to Whalen (1979a), nine of the species of sect. *Androceras* are taprooted annual herbs with wide edaphic tolerances. *Solanum johnstonii*, *S. tenuipes*, and *S. tribulosum*, however, are calciphilic herbaceous perennials. Judging from their widely separated positions on the molecular trees, it appears that the latter traits evolved independently in the three species.

Biogeographical Relationships—Based on his interpretation of cladistic relationships in sect. *Androceras*, Whalen

(1979a) considered ser. *Androceras* to be plesiomorphic within the section, implying an origin for the section in the central Mexican highlands (Whalen 1979a, 1983). However, the molecular phylogenies place *S. tenuipes*, included in ser. *Violaceifolium* by Whalen (1979a), as sister to the remainder of sect. *Androceras* with good support (82% BS, 1.0 PP). *Solanum tenuipes* occurs in the northern Chihuahua Desert near the Texas-Mexico border, pointing to a more northerly origin for the section. In the BI trees, the Glandulosa clade is in turn sister to the remainder of the species (Fig. 2). Species of this clade are also found in the northern Chihuahua Desert and range into the southwestern U. S. A., consistent with a northern origin. However, this latter relationship is poorly supported and collapses in the MP strict consensus trees. Nonetheless, molecular evidence refutes Whalen's (1979a, 1983) hypothesis of a central to southern Mexican origin for sect. *Androceras*.

Clades Within sect. Androceras—Rostratum clade—The Rostratum clade contains *S. rostratum*, *S. fructo-tecto*, and *S. angustifolium*, three of the five species placed by Whalen (1979a) in ser. *Androceras*. *Solanum rostratum* is a widely introduced weed and is common in the central and western U. S. A., but Whalen (1979a) considered central Mexico to be its area of origin due to the high level of morphological variability in this region and because many of the sister taxa proposed by Whalen (1979a) occur there. Our phylogeny samples accessions from both the U. S. A. and Mexico and all form a strongly supported group. Combined with many morphological characters, there is little doubt that, although it is the most widespread species in the section, *S. rostratum* is a monophyletic and distinct species. The other members of the Rostratum clade have more restricted distributions: *S. fructo-tecto* is found in the vicinity of Mexico City and Ciudad Durango, and *S. angustifolium* is found from southern Mexico through Honduras. Although *S. fructo-tecto* is vegetatively similar to *S. rostratum*, Whalen did not encounter hybrids or collections intermediate between the two species in reproductive characteristics. Therefore, he states that the overlap in vegetative characteristics between the species probably represents natural variation. Whalen (1979a) considered *S. angustifolium* to be closely related to *S. rostratum* but also called it a bridging taxon between his sers. *Androceras* and *Violaceiflorum*. Our phylogeny indicates that, despite sharing trichome and flavonoid characters with species in Whalen's ser. *Violaceiflorum*, *S. angustifolium* is in fact closely related to *S. rostratum*.

Pacificum clade—The Pacificum clade is found in western Mexico along the Pacific slope of the Sierra Madre Occidental and inland in central Mexico. This clade comprises two of the three species placed by Whalen (1979a) in ser. *Pacificum*; *S. leucandrum*, the third, was not sampled. *Solanum grayi* has been divided into two varieties based on flower size. The small-flowered form is known as *S. grayi* var. *grayi*, whereas the large-flowered plants are segregated as var. *grandiflorum*. Our phylogeny sampled species from throughout the range of *S. grayi* and did not consistently separate these varieties. These varieties seem to have arisen from character displacement in areas where *S. grayi* occurs sympatrically with its purported sister species *S. lumholtzianum*. Whalen (1978b) showed that *S. lumholtzianum* and *S. grayi* have similar sized flowers over their distinctive ranges, but show strong character displacement where their ranges overlap in Sonora and northern Sinaloa, with the flowers of *S. grayi* much smaller there than in other parts of its range. *Solanum grayi* and *S. lumholtzianum* were shown to successfully hybridize in experimental crosses, but Whalen (1978b, 1979a) posits mechanical isolation via character displacement of floral traits in areas where the two species overlap, indicating that in nature they would not share the same pollinators and would effectively be reproductively isolated. Although our phylogenetic data suggest that the varietal distinctions in *S. grayi* might not be warranted, additional sampling from this species is needed to examine this question. The final member of Whalen's ser. *Pacificum*, *S. leucandrum*, is a rarely collected species and thus material was not available for this study. It is endemic to western Puebla and is morphologically similar to *S. grayi*, thus would likely be included in the Pacificum clade.

Setigeroid clade—The Setigeroid clade is strongly supported in our phylogeny and contains *S. davisense*, *S. citrullifolium* vars. *citrullifolium* and *setigerum*, and *S. heterodoxum* var. *setigeroides*. These species all occur in the southwestern U. S. A. and the area along the Texas-Mexico border. Our phylogeny shows that *S. davisense* is closely related to *S. citrullifolium* var. *citrulllifolium* (76% BS, 1.0 PP), a result supported by allozyme data from Whalen (1979b). *Solanum davisense* is distinct from the other species of the Setigeroid clade due a more erect habit, acutely lobed leaves, smaller flowers, and smooth unridged seeds as well as chemical differences (Whalen 1979a). Divergence of *S. davisense* and *S. citrullifolium* was likely due to the slight geographical separation of *S. davisense* at the margin of the range of *S. citrullifolium* var. *citrulllifolium* (Whalen 1979a, 1979b). *Solanum citrullifolium* vars. *setigerum* and *citrullifolium* do not form a monophyletic group in either the MP or BI combined analysis. Monophyly of *S. citrullifolium* var. *setigerum* itself is not supported in the MP strict consensus tree, yet it receives strong support (1.0 PP) in the BI 50% majority rule tree. Therefore, it is unclear whether the two varieties should be recognized as taxonomically distinct entities. As indicated by the common varietal name *setiger-* (Latin for "bristly"), *S. citrullifolium* var. *setigerum* and *S. heterodoxum* var. *setigeroides* share morphological similarities and have also been found to have a history of hybridization (Whalen 1979a). This, combined with the phylogenetic relatedness of these taxa, warrants a more detailed taxonomic investigation of these species and varieties to determine the relationship and specific delimitations of members of the Setigeroid clade.

Glandulosa clade—The Glandulosa clade presents interesting taxonomic and biogeographic problems. This clade contains *S. citrullifolium* var. *knoblichii*, *S. heterodoxum* var. *novomexicanum* and an unidentified species here called "Elder 46" based on the collector and collection number. *Solanum citrullifolium* var. *knoblichii* morphologically resembles var. *citrullifolium* but is restricted to western Chihuahua state in Mexico. It has longer hairs and more spreading fruit pedicels than the other varieties of *S. citrullifolium* but, due to a lack of collections, other morphological differences are not apparent. It is distantly related to its conspecifics, which occur in the Setigeroid clade (see above), and deserves further collection and taxonomic study. *Solanum heterodoxum* var. *novomexicanum* was given specific status [as *Androcera novomexicana* (Bartlett) Wooten & Standl.] by Wooten and Standley (1913). Despite the large geographic separation between *S. heterodoxum* var. *heterodoxum* from the area around Mexico City and var. *novomexicanum* from New Mexico, Whalen (1979a) felt that these varieties resembled each other except for the more stellate corollas in the latter variety. The geographically close *S. heterodoxum* var. *setigeroides* occurs in adjacent areas of New Mexico, Arizona, and the Texas-Mexico border. This variety

is distinct morphologically, with densely prickly stems and much finer spines than the other varieties of *S. heterodoxum*. Given the distinct morphological traits and the phylogenetic distance between *S. heterodoxum* var. *novomexicanum* and the other varieties, the specific classification of Wooten and Standley (1913) should be reconsidered. The final member of this clade, "Elder 46," is a collection from Jeff Davis County, Texas. This specimen has previously been identified as *S. grayi* var. *grandiflorum*, *S. davisense*, and *S. heterodoxum* but does not fit any of those species concepts. Whalen did not examine this specimen, and use of his key and comparison to specimens he annotated does not result in a satisfactory determination. Since it appears that many of the species in the section are restricted endemics, it is possible that this collection represents an undescribed species.

The three species in the Glandulosa clade share some morphological characteristics including a diminutive weedy annual habit, violet or occasionally white flowers, and simple, often glandular hairs. Whalen (1979a) notes that the flavonoid profile for *S. heterodoxum* var. *novomexicanum* is identical to that of var. *heterodoxum*; however, the other members of the Glandulosa clade have not been sampled. The species in the Glandulosa clade have geographic ranges that do not appear to overlap, with "Elder 46" occurring in Jeff Davis County, Texas, *S. heterodoxum* var. *novomexicanum* occurring in north central New Mexico, and *S. citrullifolium* var. *knoblichii* restricted to Chihuahua, Mexico. Further systematic study and field collections will help to clarify the number of distinct taxa represented within this clade.

Solanum johnstonii—The two accessions of *S. johnstonii* emerge as a monophyletic group. This species has a very restricted range in the Durango state of north-central Mexico and has often been identified as *S. rostratum*. However, Whalen (1979a) cites many morphological differences as well as reproductive isolation as evidence that *S. johnstonii* and *S. rostratum* are distinct species. Our phylogeny supports this separation, but there is little support for the relationship of *S. johnstonii* with any of the other clades within sect. *Androceras*.

Solanum tribulosum—*Solanum tribulosum* shares purple flower color with members of the Whalen's ser. *Violaceifolium*, but he placed it in ser. *Androceras* due to geographical distribution, chemical characteristics (notably a lack of 8-hydroxyflavonoids and various flavones that are found in ser. *Violaceifolium*) and morphological features such as stellate corollas and smooth seeds. Results from the combined analyses indicate that *S. tribulosum* is more closely related to the other purple-flowered taxa here placed in the Setigeroid clade than to the species of Whalen's ser. *Androceras*, which include *S. rostratum*, *S. fructo-tecto*, and *S. angustifolium* (Rostratum clade) as well as *S. johnstonii*.

Solanum heterodoxum var. *heterodoxum*—The position of *S. heterodoxum* var. *heterodoxum* within the section is unresolved and it is not placed with either of the other *S. heterodoxum* varieties. This isolated phylogenetic position mirrors its geographical disjunction; *Solanum heterodoxum* vars. *setigeroides* and *novomexicanum* occur in the southwestern U. S. A., and northern Mexico, whereas var. *heterodoxum* is greatly disjunct in central Mexico. *Solanum heterodoxum* var. *heterodoxum* has less prickly stems with much stouter prickles than those of var. *setigeroides* and flowers with much more interpetalar tissue than those of var. *novomexicanum*. These differences, along with the phylogenetic results, indicate that *S. heterodoxum* as currently defined is almost certainly not monophyletic.

Solanum tenuipes—The two varieties of *S. tenuipes* are placed together as a strongly supported monophyletic group sister to all the other taxa of sect. *Androceras*. This species is found along the Texas-Mexico border and is divided into var. *tenuipes* and var. *latisectum* based on geography, leaf dissection, and seed size. Whalen (1979a) notes intermediates between these varieties and our phylogeny gives only weak support to grouping the two accessions of var. *tenuipes* (69% BS, 0.80 PP). Whalen (1979a) considered *S. tenuipes* to be derived within the section, making the placement of *S. tenuipes* at the base of sect. *Androceras* unexpected and worthy of further investigation.

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Appendix 1. Summary of species, collection location, vouchers, and GenBank accession numbers for taxa used in this study provided in the order ITS, *waxy*, and *trnT-F*. Asterisks indicate specimens identified by M. D. Whalen. NIJ – cultivated at Radboud University, Nijmegen, The Netherlands.

S. *acerifolium* Dunal - Costa Rica, *Bohs 2714* (UT); AY561261, AY562949, AY266149. **S. *augustifolium*** Mill. - Oaxaca, Mexico, *Whalen 2* (LL)*; GQ143645, GQ143677, GQ149729. **S. *bahamense*** L. - NIJ 944750187, *Bohs 2936* (UT); AY996487, AY996386, GQ149730. **S. *betaceum*** Cav. – Bolivia, *Bohs 2468* (UT); AF244713, AY996387, DQ180426. **S. *carolinense*** L. – U. S. A., *Cipollini s. n.* (UT); AY996491, AY996392, DQ180476. **S. *citrullifolium* var. *citrullifolium*** - Burnet Co., Texas, *Urbatsch 4834* (NY); GQ143647, GQ143679, GQ149732. NIJ 894750197, *Bohs 3452* (UT); GQ143646, GQ143678, GQ149731. **S. *citrullifolium* var. *knoblichii*** Whalen - Chihuahua, Mexico, *Lebgue 3266* (NY); GQ143648, GQ143680, GQ149733. **S. *citrullifolium* var. *setigerum*** Bartlett - Chihuahua, Mexico, *Whalen 365* (LL)*; GQ143650, GQ143682, GQ149735. Presidio Co., Texas, *Turner 24-245* (TEX); GQ143649, GQ143681, GQ149734. **S. *crinitum*** Lam. – Brazil, *Agra et al. 7028* (JPB); GQ143651, GQ143683, GQ149736. Guyana, *Stern 255* (UT); GQ143652, GQ143684, GQ149737. **S. *davisense*** Whalen - North population Jeff Davis Co., Texas, *Board s. n.* (NY); GQ143654, GQ143686, GQ149739. South population Jeff Davis Co., Texas, *Whalen 216* (LL)*; GQ143653, GQ143685, GQ149738. **S. *"Elder 46"*** - Jeff Davis Co., Texas, *Elder 46* (TEX); GQ143655, GQ143687, GQ149740. **S. *ensifolium*** O. E. Schulz - Puerto Rico, *Bohs 2461* (UT); AY996506, AY996409, DQ180483. **S. *fructo-tecto*** Cav. - Distrito Federal, Mexico, *Iltis 28607* (NY); GQ143656, GQ143688, GQ149741. **S. *grayi* var. *grandiflorum*** Whalen - Jalisco, Mexico, *Guadalupe Ayala #91-9* (TEX); GQ143658, GQ143691, GQ149743. Sinaloa, Mexico, *Vallejo-Marin 07s195* (MEX); GQ143659, GQ143690, GQ149744. Sinaloa, Mexico, *Whalen 190* (LL)*; GQ143657, GQ143689, GQ149742. **S. *grayi* var. *grayi*** - Sonora, Mexico, *Reina 99-469* (TEX); GQ143660, GQ143692, GQ149745. **S. *heterodoxum* var. *heterodoxum*** - San Luis Potosí, Mexico, *Fryxell 3810* (NY); GQ143661, GQ143693, GQ149746. **S. *heterodoxum* var. *novomexicanum*** Bartlett - San Miguel Co., New Mexico, *Whalen 224* (LL)*; GQ143662, GQ143694, GQ149747. **S. *heterodoxum* var. *setigeroides*** Whalen - Cantron Co., New Mexico, *Shelton 127* (NY); GQ143664, GQ143696, GQ149749. Cochise Co., Arizona, *McGill 6785* (TEX); GQ143663, GQ143695, GQ149748. Sonora, Mexico, *Minckley s. n.* (UT) ; GQ143665, GQ143697, GQ149750. **S. *johnstonii*** Whalen - Coahuila, Mexico, *Villarreal 4404* (TEX); GQ143666, GQ143698, GQ149751. Durango, Mexico, *Villarreal 6246* (TEX); GQ143667, GQ143699, GQ149752. **S. *lumholtzianum*** Bartlett - Sonora, Mexico, *Reina 99-398* (TEX); GQ143668, GQ143700, GQ149753. **S. *lycocarpum*** A. St.-Hil. – Paraguay, *Bohs 3212* (UT); AY996525, AY996435, DQ812107. **S. *mitlense*** Dunal – Mexico, *Whalen & Velasco 825* (BH); AY996530, AY996442, DQ812108. **S. *myriacanthum*** Dunal - NIJ 814750043, *Cipollini 83* (UT); AY561267, AY562960, AY559240. **S. *rostratum*** Dunal - Boulder Co., Colorado (no voucher); AY996550, AY996463, DQ180489. NIJ 934750126, *Cipollini 173* (UT); GQ143670, GQ143702, GQ149755. Puebla, Mexico, *Cipollini 184* (UT); GQ143669, GQ143701, GQ149754. **S. *sendtnerianum*** Van Heurck & Müll. Arg. – Brazil, *Lepsch de Cunha & Wang 310* (MO); GQ143671, GQ143703, GQ149756. **S. *sisymbriifolium*** Lam. – Bolivia, *Cipollini 132* (UT); AY561271, AY562967, AY266235. **S. *tenuipes* var. *latisectum*** Whalen - Chihuahua, Mexico, *Whalen 72* (LL)*; GQ143672, GQ143705, GQ149757. **S. *tenuipes* var. *tenuipes*** - Brewster Co., Texas, *Whalen 218* (LL)*; GQ143673, GQ143706, GQ149758. Nuevo León, Mexico, *Hinton 22874* (TEX); GQ143674, GQ143704, GQ149759. **S. *tribulosum*** Schauer - Guanajuato, Mexico, *Ventura 8236* (TEX); GQ143675, GQ143707, GQ149760. Veracruz, Mexico, *Whalen 18* (LL)*; GQ143676, GQ143708, GQ149761. **S. *wrightii*** Benth. - Costa Rica, *Bohs 2445* (UT); GQ480731, GQ480733, GQ480732.

CHAPTER 3

MOLECULAR DELIMITATION OF CLADES WITHIN THE NEW WORLD SPECIES OF THE "SPINY SOLANUM" (*SOLANUM* SUBGENUS *LEPTOSTEMONUM*)

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Molecular delimitation of clades within New World species of the "spiny solanums" (*Solanum* subg. *Leptostemonum*)

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Abstract *Solanum* subg. *Leptostemonum* contains approximately 350–450 species, including the cultivated eggplant, *S. melongena*. Most species placed in this subgenus form a monophyletic group, the Leptostemonum clade, characterized by the presence of stellate hairs and prickles, leading to the common name of "spiny solanums". Here we present a phylogenetic analysis that circumscribes the major clades within the spiny solanums and examines the relationships among them, with an emphasis on New World species. Of particular interest is the clarification of the clade limits and species composition of groups that have not been well-sampled. We also increase sampling of taxa that have been previously analyzed in molecular studies, namely those in the Torva, Micracantha, and Erythrotrichum clades. These groups have convergent morphological characteristics that have challenged taxonomists, making classification difficult. Results from our study delimit 14 clades within the spiny solanums, including the newly designated Asterophorum, Gardneri, Sisymbriifolium, and Thomasiifolium clades. We also establish the placement of species not previously sampled, especially those endemic to Brazil. These results give an increased understanding of the evolution of the Leptostemonum clade by defining monophyletic groups within it and identify areas of the phylogenetic tree that remain unresolved and require further taxon sampling.

Keywords granule-bound starch synthase (GBSSI); ITS; *Leptostemonum*; Solanaceae; *Solanum*; *trnT-F*; *waxy*

Supplementary Material Figures S1–S3 are available in the free Electronic Supplement to the online version of this article (http://www.ingentaconnect.com/content/iapt/tax).

INTRODUCTION

Solanum L. (Solanaceae), with approximately 1400 species, is one of the 10 largest genera of flowering plants and contains economically important species such as the tomato (*S. lycopersicum* L.), eggplant (*S. melongena* L.), and potato (*S. tuberosum* L.) (Frodin, 2004; Bohs, 2005). Recent studies have aimed to resolve phylogenetic relationships within *Solanum* as well as clarify species-level taxonomy (Knapp & al., 2004; Bohs, 2005; Weese & Bohs, 2007; www.solanaceaesource.org). Analyses of DNA sequence data have helped to identify the major monophyletic groups within *Solanum*, the largest of which is the Leptostemonum clade with approximately 350–450 species (Bohs, 2005; Levin & al., 2006). This clade is characterized by the presence of stellate hairs and prickles, leading to the common name of "spiny solanums". The Leptostemonum clade largely conforms to the traditionally recognized *Solanum* subg. *Leptostemonum* (Dunal) Bitter with the exclusion of the *S. wendlandii* and *S. nemorense* species groups, whose members lack stellate hairs (Whalen, 1984; Levin & al., 2006). Hereafter, we will refer to this group as the Leptostemonum clade.

The species of the Leptostemonum clade have a worldwide distribution. Whalen (1984) notes three centers of diversity, including the Neotropics (ca. 250 spp.), Africa (ca. 80 spp.), and Australia (ca. 150 spp.). Previous authors have used morphological characters to define groups within the spiny solanums. D'Arcy (1972) recognized 22 sections; however, because he did not explicitly state species composition of these groups, comparison with other classifications is difficult. Whalen's (1984) treatment informally recognized 33 species groups with 36 species left unplaced. Nee (1999) treated only the New World species of spiny solanums, which are the major focus of this study, and placed them into 10 sections. Because we are primarily concerned with delimiting clades, elucidating their species composition, and placing previously unsampled taxa in a phylogenetic tree, we will refer to Whalen's (1984) and Nee's (1999) classifications since they both explicitly specify which species belong in each of their groups.

Levin & al. (2006) sampled species of the Leptostemonum clade from throughout its distribution for three molecular markers, the chloroplast *trnS-G* and the nuclear ITS and GBSSI or *waxy*, to construct a molecular phylogeny of the spiny solanums. This study delimited the Leptostemonum clade and defined 10 major clades within it. One of these clades is composed exclusively of taxa from the Old World. The Old World clade is the topic of other studies (Martine & al., 2006; L. Bohs & al., unpub. data) and only a few representatives are included here as placeholders. Within the New World, nine well-supported clades were designated, but the relationships among them were not well resolved (Levin & al., 2006). In addition to its utility as an overview, Levin & al. (2006) also

included more exhaustive data for specific clades, such as the Lasiocarpa and Acanthophora clades (Bohs, 2004; Levin & al., 2005).

A goal of the current study is to increase taxon sampling for many of the large groups underrepresented in Levin & al. (2006) with an emphasis on New World species. Our phylogenetic analysis targets species from sections that have not previously been studied, such as sect. *Polytrichum* (Whalen) Child, and samples more intensively from three clades that were previously underrepresented in molecular studies (the Torva, Micracantha, and Erythrotrichum clades). These groups have unclear limits and species compositions that have varied in previous classifications. In Nee's (1999) classification, these three clades account for 82 of the 185 species (44%) of the New World spiny solanums. Additionally, our phylogenetic analysis samples from geographic areas that have been underrepresented, including Brazil and the Caribbean, and specifically targets species in sect. *Polytrichum* and sect. *Persicariae* Dunal that are endemic to these areas.

In this paper, we also aim to increase resolution and support of clades within the spiny solanums by using a longer and more variable chloroplast marker, *trnT-F*, in place of *trnS-G* used in Levin & al.'s (2006) study. Comparisons of large scale phylogenies within the genus *Solanum* show that *trnT-F* is nearly twice the length and contains almost twice the number of parsimony-informative characters than *trnS-G* (Levin & al., 2005, 2006; Weese & Bohs, 2007). We compare our phylogenetic results with previous morphological classifications, and, where possible, identify morphological characters associated with each clade.

■ MATERIALS AND METHODS

Taxon sampling. — This study sampled 102 taxa from the Leptostemonum clade. These represent 44 of the 112 species (39%) of the clade sampled in Levin & al. (2006). We sampled 58 additional species of spiny solanums from groups that were not well represented in Levin & al. (2006). Selected species from clades that Levin & al. (2006) sampled extensively or that are the focus of other studies were included only to show their higher-level relationships. These groups include the Lasiocarpa clade (Bohs, 2004), the Acanthophora clade (Levin & al., 2005), the Androceras clade (Stern & al., 2010), and the Old World clade (Martine & al., 2006; L. Bohs & al., unpub. data). Focal groups of this study include the Torva, Micracantha, and Erythrotrichum clades. The spiny species *S. polygamum* Vahl was placed within the Leptostemonum clade in Levin & al. (2006) but was not resolved within any of the major clades. It was excluded from this study because its sequences were divergent for all sampled markers, making unambiguous alignment difficult. Spiny solanums in the *S. wendlandii* and *S. nemorense* species groups that have been shown to lie outside of the Leptostemonum clade (Levin & al., 2006) were also included. Non-spiny *Solanum* species in the Geminata (*S. argentinum*, *S. pseudocapsicum*, *S. arboreum*), Brevantherum (*S. abutiloides* and *S. cordovense*), Cyphomandra (*S. betaceum*, *S. diploconos*, *S. glaucophyllum*), Morelloid (*S. ptychanthum*), and Dulcamaroid (*S. dulcamara*) clades sensu Bohs (2005) and Weese & Bohs (2007) were included as outgroups and the tree was rooted using *S. laciniatum*, a member of the Archaesolanum clade, which was previously shown to be even more distantly related to the spiny solanums (Levin & al., 2006; Weese & Bohs, 2007). All taxa, along with voucher information and GenBank accession numbers, are listed in the Appendix.

DNA extraction, amplification, and sequencing. — Total genomic DNA was extracted from fresh, silica gel-dried, or herbarium material using the DNeasy plant mini extraction kit (Qiagen, Valencia, California, U.S.A.). PCR amplification for each gene region followed standard procedures described in Taberlet & al. (1991), Bohs & Olmstead (2001), and Bohs (2004) for the *trnT-L* and *trnL-F* intergenic spacer regions; Levin & al. (2005) for *waxy*; and Levin & al. (2006) for ITS. The ITS region was amplified as a single fragment using primers ITSleu1 (Bohs & Olmstead, 2001) and ITS4 (White & al., 1990) using PCR conditions described in Bohs & Olmstead (2001). When possible, *trnT-F* and *waxy* were amplified as single fragments using primers a and f for *trnT-F* (Taberlet & al., 1991) and primers waxyF and waxy2R for *waxy* (Levin & al., 2005). PCR conditions for *trnT-F* followed Bohs & Olmstead (2001); conditions for *waxy* followed Levin & al. (2005). When necessary, overlapping fragments were amplified and assembled, using primers a with d, and c with f to amplify *trnT-F*, and primers waxyF with 1171R, and 1058F with 2R to amplify *waxy*.

PCR products were cleaned using the Promega Wizard SV PCR Clean-Up System (Promega Corporation, Madison, Wisconsin, U.S.A.). The University of Utah DNA Sequencing Core Facility performed sequencing on an ABI automated sequencer. Sequences were edited in Sequencher v.4.8 (Gene Codes Corp., Ann Arbor, Michigan, U.S.A.) and all new sequences were submitted to GenBank (Appendix).

Sequence alignment and analyses. — Sequence alignments for all of the gene regions were straightforward and performed visually using Se-Al v.2.0a11 (Rambaut, 1996). The aligned datasets and representative phylogenetic trees are available in TreeBASE (S11233). Missing data comprised 0.00062% of the combined data matrix (286 of 462,031 total bases).

Parsimony analyses were performed on each dataset separately and on the combined dataset using PAUP* v.4.0b10 (Swofford, 2002). All characters were weighted equally in analyses that implemented tree bisection and reconnection (TBR) branch swapping with 1000 heuristic random-addition replicates, each limited to 1,000,000 swaps per replicate. Gaps were treated as missing data. Bootstrapping (BS; Felsenstein, 1985) was used to evaluate branch support with 1000 random-addition replicates and TBR branch swapping limited to 1,000,000 swaps per replicate. Datasets were further analyzed using TNT v.1.0 (Goloboff & al., 2008) to search for shorter trees than were obtained in standard PAUP* analyses. One thousand heuristic partition homogeneity replicates were completed, each with 10 random-addition sequence replicates, TBR branch-swapping, MulTrees off, and gaps treated as missing data.

Prior to Bayesian analyses, a general model of nucleotide evolution was selected for both the separate and the combined datasets using the Akaike information criterion identified in Modeltest v.3.7 (Posada & Crandall, 1998). MrBayes v.3.1 (Huelsenbeck & Ronquist, 2001) was used to analyze each of the separate and combined datasets. For each analysis, five million generations were run using eight Markov chains, each initiated from a random tree and sampled every 1000 generations. Each of the analyses reached a standard deviation below 0.01 between the chains and all parameters from each analysis were visualized graphically to determine the trees discarded as burn-in prior to achieving stationarity. The Bayesian analysis reached stationarity and the first 500,000 generations were eliminated as burn-in in all analyses.

RESULTS

Phylogenetic analyses. — The parsimony strict consensus and Bayesian majority-rule consensus trees of all datasets differed only in the degree of resolution, with Bayesian tree topologies more resolved than parsimony trees (Table 1). Clades with low posterior probabilities (PP), typically those below 0.90 PP but occasionally those with up to 1.0 PP in Bayesian analyses were often collapsed in parsimony strict consensus trees. Descriptive statistics for individual and combined genes are provided (Table 1). More nodes were strongly supported by combining the data than were obtained in any of the separate analyses.

Topological conflicts. — In parsimony analyses, each DNA sequence region consistently identified the same major, well-supported clades comprising identical species groups, but relationships among major clades were often not strongly supported (BS < 90%), or were unresolved, and thus cannot be considered conflicting under Wiens' (1998) criteria. The Bayesian analyses of individual datasets gave some conflicting nodes (cutoff at < 0.95 PP). However, posterior probabilities are known to be inflated relative to bootstrap values (Cummings & al., 2003; Erixon & al., 2003; Simmons & al., 2004). Our discussion will be based on the parsimony strict consensus tree of the combined dataset, which is a conservative hypothesis of phylogenetic relationships (Fig. 1). The parsimony strict consensus trees for the individual markers (Figs. S1–S3) are presented in the Electronic Supplement.

Higher level phylogenetic relationships. — The Leptostemonum clade emerges as monophyletic and strongly supported (100% BS, 1.0 PP). Its overall topology is similar to that of Levin & al. (2006) but our increased taxon sampling and the use of the more informative *trnT-F* marker has given a more resolved backbone and more strongly supported nodes. Our results support the exclusion of the *S. wendlandii* and *S. nemorense* species groups from the Leptostemonum clade as proposed by Levin & al. (2006). These taxa were traditionally placed in *Solanum* subg. *Leptostemonum* because they have prickles. However, the absence of stellate hairs as well as molecular data support their exclusion from the Leptostemonum clade.

With respect to the relationships among the major groups in the Leptostemonum clade, phylogenetic results place the Gardneri clade as sister to the Erythrotrichum + Thomasiifolium clades (99% BS, 1.0 PP). This clade in turn is sister to the remainder of the sampled members of the Leptostemonum clade, which form a monophyletic group with strong support (94% BS, 1.0 PP). Within this latter clade, the Acanthophora and Lasiocarpa clades are sister to each other (85% BS, 1.0 PP). The Androceras/Crinitum clade is weakly supported (63% BS, 1.0 PP) and is weakly supported as sister to the Sisymbriifolium clade (61% BS, 1.0 PP). The Old World clade is weakly supported as sister to the Elaeagnifolium clade (62% BS, 1.0 PP). These two clades plus the New World species *S. hieronymi* form a strongly supported monophyletic group (99% BS, 1.0 PP). The relationships among the Torva, Micracantha, Carolinense, Asterophorum, and Bahamense clades remain unclear. These groups, along with three species unassigned to the 14 major clades, *S. campechiense*, *S. crotonoides*, and *S. multispinum*, form a large but unsupported polytomy.

Sectional level relationships. — The Leptostemonum clade is comprised of 14 large, well-supported clades (63%–100% BS, all 1.0 PP), which largely correspond to those of Levin & al. (2006). There are four taxa that remain unassigned to the 14 clades, *S. campechiense*, *S. crotonoides*, *S. hieronymi*, and *S. multispinum* (arrows, Fig. 1). Table 2 provides a summary of the recognized clades with their bootstrap and posterior probability support values and compares the clade species composition with the species groups of Whalen (1984) and sections of Nee (1999). Each clade is discussed in more detail below.

Table 1. Descriptive statistics for each dataset analyzed. Strongly supported nodes for parsimony indicate those with ≥90% BS; Bayesian strongly supported nodes are those with ≥0.95 PP.

Data partition	Aligned sequence length	Parsimony informative characters	Most parsimonious trees	Tree length	Consistency index	Retention index	Strongly supported nodes, parsimony	Model selected	Strongly supported nodes, Bayesian
ITS	711	245	209	1747	0.361	0.660	21	TIM+I+G	54
waxy	2231	505	19,579	1606	0.691	0.838	46	TVM+G	79
trnT-F	2137	224	385,577	706	0.817	0.875	27	GTR+I+G	63
Combined	5079	974	209	4223	0.549	0.742	61	GTR+I+G	82

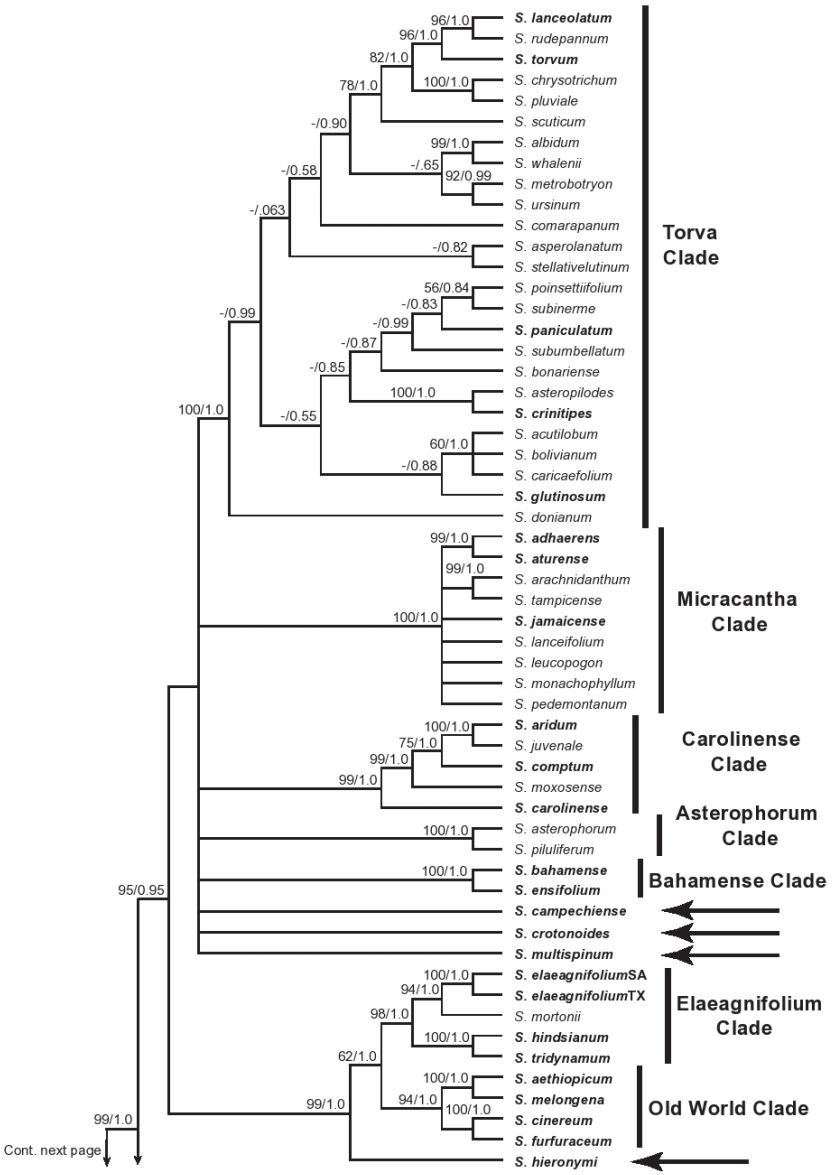
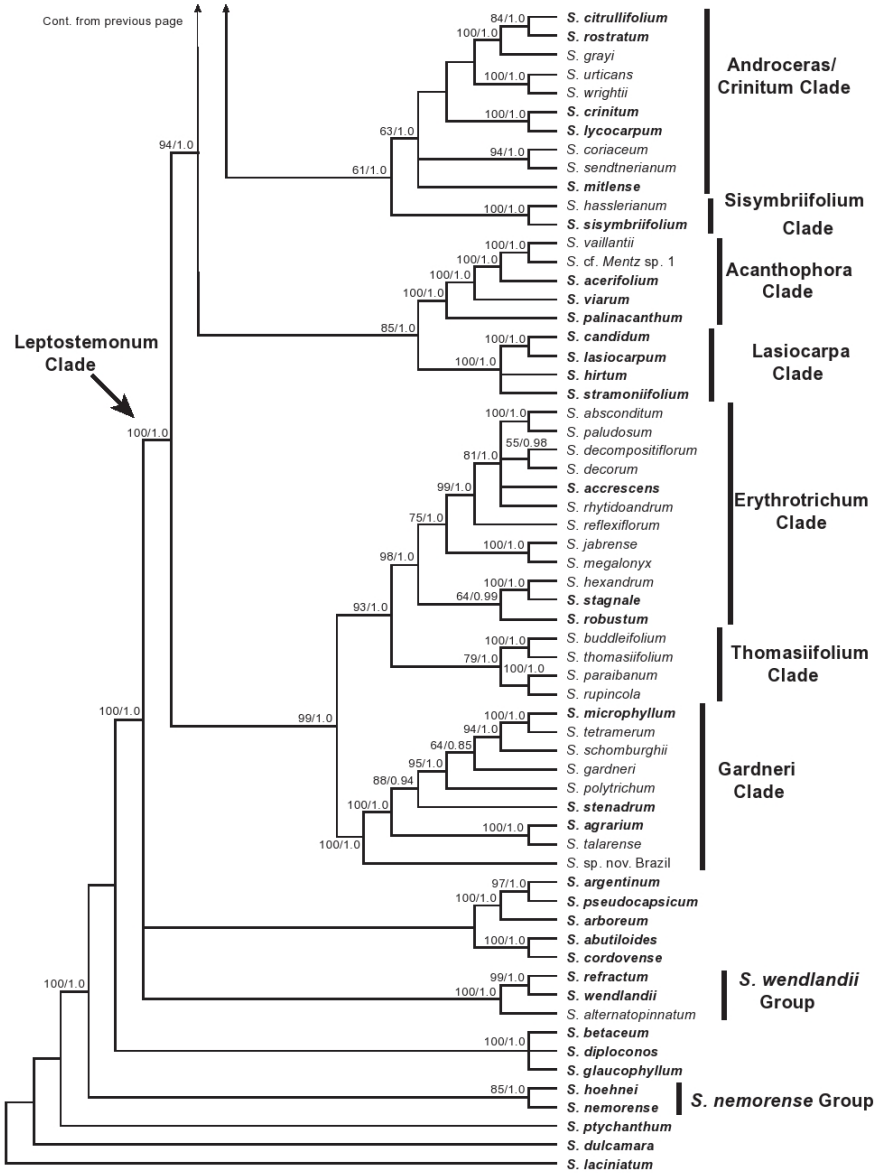


Fig. 1. Strict consensus of 209 most parsimonious trees obtained from the combined analysis of the *trnT-F*, *waxy*, and ITS data. Numbers above branches are bootstrap values over 50% followed by posterior probabilities from Bayesian analysis. Species names in bold italics are those sampled in Levin & al. (2006); species in italics are those new to this study. The clades discussed in the text are labeled. The four taxa that are ►



▶ unplaced within the 14 clades are indicated by arrows. Taxa in the spiny *S. nemorense* and *S. wendlandii* species groups that are not members of the Leptostemonum clade are labeled, whereas non-spiny outgroups are not labeled. The abbreviations SA and TX for *S. elaeagnifolium* refer to specimens from South America and Texas, respectively.

Table 2. Summary of the 14 clades recognized here with support values. The species composition of each clade is compared with Whalen's (1984) species groups and Nee's (1999) sections. Asterisks indicate instances where representatives from a species group or section are included in more than one clade or emerge in multiple places on the tree. See Discussion for further details.

Clade name (bootstrap support, posterior probability)	Species groups of Whalen (1984) included	Sections of Nee (1999) included
Torva (100% BS, 1.0 PP)	*S. torvum* species group, *S. subinerme* species group, 1 species not treated	Sect. *Torva*, Sect. *Micracantha**
Micracantha (100% BS, 1.0 PP)	*S. lanceifolium* species group, 1 unplaced species	Sect. *Micracantha**
Carolinense (99% BS, 1.0 PP)	*S. multispinum* species group*, 1 unplaced species	Sect. *Melongena**
Asterophorum (100% BS, 1.0 PP)	*S. asterophorum* species group	Sect. *Polytrichum**, 1 species not treated
Bahamense (100% BS, 1.0 PP)	*S. bahamense* species group	Sect. *Persicariae**
Elaeagnifolium (98% BS, 1.0 PP)	*S. ellipticum* species group*, *S. vespertilio* species group*, 1 species not treated, 1 species unplaced	Sect. *Melongena**
Old World (94% BS, 1.0 PP)	Various species groups	Mainly sect. *Melongena**
Androceras/Crinitum (63% BS, 1.0 PP)	*S. rostratum* species group, *S. crinitum* species group, 1 unplaced species, 2 species not treated	Sect. *Androceras*, Sect. *Crinitum*, Sect. *Micracantha**
Sisymbriifolium (100% BS, 1.0 PP)	*S. polytrichum* species group*, 1 unplaced species	Sect. *Melongena**
Acanthophora (100% BS, 1.0 PP)	*S. mammosum* species group*	Sect. *Acanthophora**
Lasiocarpa (100% BS, 1.0 PP)	*S. quitoense* species group	Sect. *Lasiocarpa*
Erythrotrichum (98% BS, 1.0 PP)	*S. erythrotrichum* species group, *S. polytrichum* species group*, 5 species not treated	Sect. *Erythrotrichum**, 6 species not treated
Thomasiifolium (79% BS, 1.0 PP)	*S. polytrichum* species group*, 2 unplaced species, 1 species not treated	Sect. *Persicariae**, Sect. *Erythrotrichum**, Sect. *Micracantha**, 1 species not treated
Gardneri (100% BS, 1.0 PP)	*S. polytrichum* species group*, *S. mammosum* species group*, 3 unplaced species, 3 species not treated	Sect. *Persicariae**, Sect. *Polytrichum**, Sect. *Acanthophora**, 1 species not treated

■ DISCUSSION

Our increased taxon sampling and the use of the more phylogenetically informative *trnT-F* gene region have led to a more resolved phylogenetic tree than that of Levin & al. (2006). We recognize 14 major clades in the spiny solanums. These clades remain informally named, as further re-circumscriptions of sections within the Leptostemonum clade should await exhaustive, clade by clade studies to avoid further confusion of infrageneric taxonomy. We provide descriptions of the major clades below with details of their geographical distribution, morphological characters, and, when possible, estimates of expected species numbers. Provisional species lists for these clades can be found on the Solanaceae Source webpage (www.solanaceaesource.org).

Of particular importance in this study is the division of the Robustum clade of Levin & al. (2006) into the Erythrotrichum, Thomasiifolium, and Gardneri clades. Their study suggested two strongly supported clades within the Robustum clade, one containing *S. accrescens*, *S. robustum*, and *S. stagnale* and the other containing *S. agrarium*, *S. stenandrum*, and *S. microphyllum*. Our increased sampling confirms the presence of two well-supported clades within the Robustum clade as suggested by Levin & al. (2006), here denoted as the Erythrotrichum and Gardneri clades. Sampling of taxa not included in Levin & al. (2006) indicates the presence of a third clade, the Thomasiifolium clade.

Our study also strengthens the sister relationship of the Acanthophora and Lasiocarpa clades that was weakly supported in Levin & al. (2006). Finally, our study suggests that the Androceras/Crinitum clade is sister to the Sisymbriifolium clade. While these results help to clarify the relationships within the Leptostemonum clade, there remains a largely unresolved group that involves many of the most speciose clades,

including the large Torva clade and the very diverse Old World clade. Further study with more molecular data is underway in an attempt to resolve relationships in this portion of the tree (S. Stern & L. Bohs, unpub. data).

Torva clade. — We have greatly increased the sampling of the Torva clade from the 5 species used in Levin & al. (2006) to 25 species. The Torva clade corresponds to Whalen's (1984) *S. torvum* species group and Nee's (1999) sect. *Torva* Nees, which are concordant in circumscription and contain approximately 45 species. The Torva clade is consistent with Whalen and Nee's concepts but also includes *S. poinsettiifolium* and *S. subinerme*. Whalen (1984) placed *S. subinerme* in his *S. subinerme* species group and did not treat *S. poinsettiifolium*. Nee (1999) placed the two species together in sect. *Micracantha* Dunal.

Members of the Torva clade are scandent to erect shrubs or small trees with usually branched inflorescences, straight or occasionally recurved spines, stellate corollas with narrow triangular lobes and often abundant interpetalar tissue, and small to medium-sized leathery berries with mucilaginous pulp. The Torva clade is found throughout the Neotropics but is most diverse in the Andes and is characteristic of secondary vegetation and grazed land, with some species, most notably *S. torvum*, being noxious weeds in the Old World. *Solanum poinsettiifolium* and *S. subinerme* have recurved prickles, simple inflorescences, and curved buds and anthers, leading Whalen (1984) and Nee (1999) to exclude them from the *S. torvum* species group and sect. *Torva*, respectively, though both authors noted their probable affinities with these groups. These species have narrowly triangular corolla lobes and leathery mucilaginous berries typical of the Torva clade and are clearly placed within it on the basis of molecular data.

Within the Torva clade there is little bootstrap support for many of the higher-level nodes; however, many of the sister species relationships are strongly supported. Clarification of the relationships in this group will undoubtedly require the use of more molecular markers.

Micracantha clade. — Nee (1999) placed 19 species within sect. *Micracantha*. We sampled 13 of these species, and 9 of these fall within the Micracantha clade, corresponding to Nee's (1999) subsection 1 series 1 and 3 and subsection 3. In contrast, Whalen (1984) included 11 species in his *S. lanceifolium* species group, and, accounting for changes in nomenclature, we sampled all of these. The species composition of the Micracantha clade recovered in our analysis is more similar to Whalen's (1984) concept of the group, with the inclusion of *S. jamaicense*, which he left as an unplaced species. Both classifications focused on the fact that the plants climb via recurved prickles; however, as noted below, these characteristics appear to have evolved multiple times.

The Micracantha clade is native to the Neotropics, ranging from south Florida through the Caribbean and Central America and tropical South America to Bolivia. Members of the clade are typically found in disturbed habitats, including river banks, swamps, and forest gaps. They have convergent traits with other groups in the Leptostemonum clade, including a viny habit and recurved prickles found in some species of the Torva clade (*S. subinerme*, *S. poinsettiifolium*), the Crinitum clade (*S. coriaceum* and *S. sendtnerianum*), and the Thomasiifolium clade (*S. paraibanum*, *S. rupincola*). Despite this convergence, members of this clade are always vines or scandent shrubs with unbranched inflorescences, strictly recurved spines, and deeply stellate corollas with strap-shaped lobes and very little interpetalar tissue. A revision of the Micracantha clade along with further phylogenetic study using additional molecular markers is clarifying the relationships within this group (S. Stern, unpub. data).

Carolinense clade. — The composition of the Carolinense clade is similar to that of Levin & al. (2006), with the addition of *S. juvenale* and *S. moxosense*. It is composed of small rhizomatous, erect or prostrate plants with abundant needle-like prickles, usually densely spiny calyces (except in *S. moxosense*), an andromonoecious reproductive system, and small to medium-sized, green to yellow mottled fruits. The group has a disjunct geographic range, with *S. carolinense* native to the southeastern United States and the other members native to arid areas of Paraguay, Argentina, and Bolivia.

Whalen (1984) placed the South American species *S. aridum* (as the synonym *S. conditum* C.V. Morton), *S. juvenale*, and *S. comptum* in his *S. multispinum* species group but kept the North American *S. carolinense* as unplaced. Nee (1999) placed *S. aridum*, *S. juvenale*, *S. comptum*, and *S. carolinense* in his sect. *Melongena* (Mill.) Dunal subsect. *Lathyrocarpum* G. Don; however, he also included *S. hasslerianum*, which our analysis places in the Sisymbriifolium clade and *S. mortonii*, which our analysis places in the Elaeagnifolium clade. Neither classification included *S. moxosense*, a Bolivian species described more recently (Nee & al., 2006). *Solanum hieronymi* and *S. multispinum* were placed with members of the Carolinense clade in Nee's (1999) sect. *Melongena* and Whalen's (1984) *S. multispinum* group due to their similarities in habitat, distribution, and morphology with species of this clade. However, our results are similar to those of Levin & al. (2006) indicating that neither *S. hieronymi* nor *S. multispinum* are supported as members of the Carolinense clade (discussed below).

Asterophorum clade. — The two representatives of the Asterophorum clade have not previously been included in phylogenetic studies. The species in this clade are native to northeastern (*S. asterophorum*) and southeastern Brazil (*S. piluliferum*) and characterized by pronounced zig-zag stems with paired and unequal leaves, small leaf-opposed inflorescences, and accrescent fruiting calyces.

The strong support for *S. asterophorum* and *S. piluliferum* as sister taxa corresponds to Whalen's (1984) *S. asterophorum* species group, which contained only these two species. Nee (1999) did not treat *S. piluliferum*, but these data refute his placement of *S. asterophorum* in sect. *Polytrichum*, as our molecular data place *S. polytrichum* in the Gardneri clade.

Bahamense clade. — Similar to the results of Levin & al. (2006), the two species in the Bahamense Clade, *S. bahamense* and *S. ensifolium* (previously referred to as *S. drymophilum* O.E. Schulz), are strongly supported as a monophyletic group. These species are found in the Caribbean, and a detailed study of the Bahamense species group has shown that it contains an

additional species, *S. polyacanthos* Lam., native to Hispaniola (Strickland-Constable & al., 2010). Although there are striking morphological differences within this group, most notably in the diminutive leaves, flowers, and fruits of *S. polyacanthos*, these species are united by their scattered needle-like prickles, deeply stellate corollas, small juicy red or black fruits on strongly recurved fruiting pedicels, and the presence of stellate hairs on the adaxial surface of the anthers, an unusual characteristic within the spiny solanums (Whalen, 1984; Strickland-Constable & al., 2010).

Whalen's (1984) *S. bahamense* species group contained six species native to the West Indies, including *S. bahamense*, *S. ensifolium*, and *S. polyacanthos*; the other three species he included are now regarded as synonyms of *S. bahamense* or *S. ensifolium* (Strickland-Constable & al., 2010). Nee (1999) treated *S. ensifolium* as a synonym of *S. bahamense* and placed it in sect. *Persicariae*, along with 14 other species. Aside from *S. bahamense*, our analysis sampled six of the species of this section and placed them in at least two different clades. Our results indicate *S. gardneri*, S. *microphyllum*, *S. schomburghii* and *S. tetramerum* are part of the Gardneri clade, *S. buddleifolium* is in the Thomasiifolium clade, and *S. crotonoides* is unassigned among the 14 clades.

Elaeagnifolium clade. — The Elaeagnifolium clade is the same as that of Levin & al. (2006) with the addition of *S. mortonii* that they did not sample. Members of this clade are rhizomatous herbs with dense, almost felt-like pubescence, purple corollas, and somewhat accrescent fruiting calyces. Species of the Elaeagnifolium clade show pronounced floral dimorphism; *S. elaeagnifolium*, *S. mortonii*, and *S. hindsianum* have flowers that are actinomorphic or nearly so, whereas those of *S. tridynamum* are zygomorphic, with three long lower and two short upper stamens in the staminate flowers (Bohs & al., 2007). *Solanum hindsianum* and *S. tridynamum* have an unusual fruit type that is erect, dry, and circumsessile or irregularly dehiscent, with the seeds dispersed passively by wind or rain action (Lester & Symon, 1989; Knapp, 2002).

Members of this clade share morphological characteristics with the Carolinense clade, such as needle-like spines, small to medium-sized yellow or greenish fruits, and an andromonoecious reproductive system in those species that have been studied, including *S. elaeagnifolium* (Martine & al., 2009), *S. mortonii* (Hunziker, 1979), and *S. tridynamum* (Bohs & al., 2007). This morphological convergence is likely due to the clades inhabiting similar arid habitats in North and South America. Like the Carolinense clade, the Elaeagnifolium clade has a large geographical disjunction, with some members found in the United States and Mexico (*S. hindsianum*, *S. tridynamum*), others in South America (*S. mortonii*), and with *S. elaeagnifolium* found in both areas.

Whalen (1984) placed *S. elaeagnifolium* in the *S. ellipticum* species group and *S. tridynamum* in the *S. vespertilio* species group. However, these groups both contained species from the Old and New World and are clearly not monophyletic since nearly all of the Old World spiny solanums form a clade (see below). Whalen left *S. hindisanum* unplaced and did not treat *S. mortonii*. Nee (1999) placed the members of the Elaeagnifolium clade in sect. *Melongena* subsect. *Lathyrocarpum*. However, this subsection also contained species that our results place in different clades, such as *S. aridum*, *S. comptum*, and *S. juvenale* (Carolinense clade), *S. hasslerianum* (Sisymbriifolium clade), and *S. hieronymi* and *S. multispinum*, which are unassigned to any of the 14 clades.

Old World clade. — The four representatives of the Old World clade included here are from Africa, Asia, and Australia, and form part of a much larger strongly supported monophyletic group that includes the majority of Old World spiny solanums (Levin & al., 2006; Weese & Bohs, 2007, 2010). This clade represents a large radiation with a wide range of phenotypes. No single or combination of morphological characters appears to define this group. The main feature defining this clade is its geographical location, as very few species of Old World spiny solanums fall outside of the Old World clade. A few notable exceptions, such as *S. torvum* of the Torva clade are introductions from the New World, whereas a few taxa such as *S. lasiocarpum* and *S. repandum* of the Lasiocarpa clade apparently represent independent radiations into the Old World from New World ancestors. Detailed study of the Old World spiny solanums is underway and will help to clarify relationships within this clade (M. Vorontsova & al., unpub. data; L. Bohs & al., unpub. data).

Androceras/Crinitum clade. — Species placed in Whalen's (1984) *S. rostratum* species group and Nee's (1999) sect. *Androceras* (Nutt.) Whalen (*S. citrullifolium*, *S. rostratum*, *S. grayi*) form a strongly supported monophyletic group nested within a larger clade of species placed in Whalen's (1984) *S. crinitum* species group and Nee's (1999) sect. *Crinitum* (Whalen) Child (*S. urticans*, *S. wrightii*, *S. crinitum*, *S. lycocarpum*). Our data also support the inclusion of the Amazonian *S. coriaceum* and *S. sendtnerianum* as well as the Mexican *S. mitlense* in the Androceras/Crinitum clade. While Whalen (1984) did not treat either *S. coriaceum* or *S. sendtnerianum*, Nee (1999) placed these species in sect. *Micracantha* based on their viny habit. However, other morphological characters, including large flowers and fruits with swellings on the fruiting calyx, support the relationship of these taxa with sect. *Crinitum*. Whalen (1984) left *S. mitlense* as an unplaced taxon but suggested it might be related to the *S. torvum* species group, whereas Nee (1999) tentatively placed it within sect. *Crinitum*, also suggesting that it might be a derived member of sect. *Torva*. These placements were likely due to the disjunct distribution of *S. mitlense* in Mexico where many species of sect. *Torva* are common, whereas the other species in sect. *Crinitum* are restricted to South America. The morphological characters of *S. mitlense*, including habit and flower, fruit, and seed size, are all typical of sect. *Crinitum* (F. Farruggia, unpub. data).

Although the parsimony strict consensus tree (Fig. 1) did not resolve the Crinitum group as monophyletic, the Bayesian analysis of our dataset (not shown) resulted in a monophyletic Androceras clade sister to a monophyletic Crinitum clade; however, the latter had low support (0.70 PP). A more detailed study of sect. *Androceras* (Stern & al., 2010) showed that the section is monophyletic and sister to a monophyletic sect. *Crinitum*, which includes *S. mitlense* and *S. sendtnerianum* (*S. coriaceum* was not sampled). This difference in our parsimony analysis

and the result of Stern & al. (2010) is likely due to the exhaustive sampling from sect. *Androceras* in the latter study, whereas here only three placeholder taxa were included from the approximately 12 species in the section. *Solanum* sect. *Crinitum* is under further morphological and molecular study (F. Farruggia, unpub. data) to examine its monophyly and the phylogenetic relationships among its component species.

Sections *Androceras* and *Crinitum* have distinct morphologies and geographic ranges, and it is expected that further studies with broader taxonomic sampling and additional molecular markers will support each as a monophyletic group. Members of sect. *Androceras* are among the most recognizable of the spiny solanums because of their distinctive zygomorphic, heterantherous, enantiostylous flowers, dry fruits with a persistent, prickly, and accrescent calyx, and their primarily north temperate distribution (Stern & al., 2010). This contrasts with sect. *Crinitum*, which is composed of large shrubs, trees, or woody vines with some of the largest flowers and fruits in the genus. Members of sect. *Crinitum* also have unique swellings on the fruiting calyx, fruits that oxidize black when cut open, and a center of diversity in tropical South America.

Sisymbriifolium clade. — The Sisymbriifolium clade contains two species, *S. sisymbriifolium* and *S. hasslerianum*, that have not previously been placed together. Both are found in Paraguay and northern Argentina but *S. sisymbriifolium* also has a broader distribution through the Andes into northern South America. These species are robust herbs or small shrubs with deeply pinnately lobed leaves and spiny, accrescent fruiting calyces. Whalen (1984) left *S. sisymbriifolium* unplaced, and he included *S. hasslerianum* in the *S. polytrichum* species group along with *S. hexandrum*, *S. polytrichum*, *S. stagnale*, and *S. urticans* that were sampled here. Our results show that the latter four species belong to three different clades, and none appear closely related to *S. hasslerianum*. Nee (1999) placed *S. sisymbriifolium* and *S. hasslerianum* in separate subsections within his sect. *Melongena*, each associated with species that emerge in other clades in the molecular phylogenies. Evidently these placements were based on convergent morphological characters and do not reflect phylogenetic relatedness.

Acanthophora and Lasiocarpa clades. — The Acanthophora clade largely corresponds to Whalen's (1984) *S. mammosum* species group and Nee's (1999) sect. *Acanthophora* Dunal, which was monographed by Nee (1979). Levin & al. (2005) showed that *S. agrarium* and *S. stenandrum*, which had traditionally been placed in sect. *Acanthophora*, clearly do not belong within this group. Our data support this exclusion but otherwise support the traditional circumscription of sect. *Acanthophora*. The Lasiocarpa clade corresponds to the *S. quitoense* species group of Whalen (1984) and Nee's (1999) sect. *Lasiocarpa* (Dunal) D'Arcy which was taxonomically revised by Whalen & al. (1981). Bohs (2004) and our data both support the monophyly of the Lasiocarpa clade.

The Acanthophora and Lasiocarpa clades are both native to the Neotropics, with a few species in the Lasiocarpa clade, including *S. ferox* L., *S. lasiocarpum*, and *S. repandum* G. Forst., and perhaps one species of the Acanthophora clade, *S. aculeatissimum* Jacq., native in the Old World (Bohs, 2004; Levin & al., 2005). The Acanthophora clade includes some of the most vicious examples of the spiny solanums, with needle-like prickles found throughout the plant and the unusual feature of exclusively simple hairs on the upper leaf surfaces in most species (Nee, 1979). The Lasiocarpa clade can be distinguished by its large, shallowly lobed leaves, unbranched inflorescences, and typically large fruits covered with stellate hairs (Whalen & al., 1981).

We chose to sample a few representative species from each clade because they were well-sampled in Levin & al. (2006), building on phylogenetic work by Bohs (2004) on the Lasiocarpa clade and Levin & al. (2005) for the Acanthophora clade. These clades were found to be sister to each other in Levin & al. (2006), but with low support (64% BS). Our analysis strongly supports the Lasiocarpa clade as sister to the Acanthophora clade (85% BS, 1.0 PP). We included two additional species not previously sampled, *S. vaillantii* and an undescribed Brazilian species which our data place in the Acanthophora clade. Whalen (1984) and Nee (1999) placed *S. vaillantii* in their *S. mammosum* species group and sect. *Acanthophora*, respectively. These groups correspond to our Acanthophora clade. The undescribed species matches the description given for *Solanum* sp. 1 in Mentz & Oliveira (2004) and a named but unpublished species included in Nee (1979). It is from southeastern Brazil and has morphological characters that are typical of the Acanthophora clade, including needle-like prickles and simple hairs on the upper leaf surfaces.

Erythrotrichum clade. —The Erythrotrichum clade is distinguished from other spiny solanum groups by its plurifoliate sympodial units, the presence of recurved prickles, a ferruginous to reddish tomentum with stellate-glandular trichomes, an andromonoecious reproductive system, and pubescent fruits with large seeds (Agra, 2008). There appear to be three centers of diversity for this group: Central America, northeastern Brazil, and the Andes of Peru and Ecuador.

As defined here, the Erythrotrichum clade is morphologically homogeneous and largely congruent with Nee's (1999) sect. *Erythrotrichum* (Whalen) Child, which included *S. accrescens*, *S. megalonyx*, *S. paludosum*, and *S. robustum*, and Whalen's (1984) *S. erythrotrichum* species group, which included *S. accrescens*, *S. decompositiflorum*, *S. decorum*, *S. megalonyx*, and *S. robustum*. Whalen (1984) did not include *S. paludosum*, *S. reflexiflorum*, and *S. rhytidoandrum* in his treatment, while Nee (1999) did not treat *S. decorum*, *S. decompositiflorum*, *S. reflexiflorum*, and *S. rhytidoandrum*. In more recent treatments, Agra (2004, 2007, 2008) listed all of these species as members of sect. *Erythrotrichum* except *S. reflexiflorum*, which she left as a species of uncertain placement; however, *S. robustum* was not included in her revision of sect. *Erythrotrichum* (Agra, 2004) or her key to the section (Agra, 2008). The Erythrotrichum clade also includes *S. absconditum* and *S. jabrense* that were described by Agra (2004, 2008) after the publications of Whalen (1984) and Nee (1999) and considered by her to belong to sect. *Erythrotrichum*.

Levin & al. (2006) sampled three species from the Erythrotrichum clade (*S. accrescens*, *S. robustum*, *S. stagnale*) and found them to form a well-supported monophyletic group included within their Robustum clade. Our increased sampling,

now encompassing 9 of the 22 species included in sect. *Erythrotrichum* by Agra (2008), reveals that they all form a well-supported monophyletic group that also includes *S. hexandrum*, *S. reflexiflorum*, *S. robustum*, and *S. stagnale* that Agra (2008) did not treat. *Solanum hexandrum* and *S. stagnale* have not been included in sect. *Erythrotrichum* by previous authors. Whalen (1984) and Nee (1999) included both species in the *S. polytrichum* species group and sect. *Polytrichum*, respectively; Agra (2007) included *S. hexandrum* in sect. *Polytrichum* but left *S. stagnale* unplaced. According to our results, these species clearly belong to the Erythrotrichum clade. Within the Erythrotrichum clade, *S. hexandrum*, *S. robustum*, and *S. stagnale* form a monophyletic group, but with poor bootstrap support. The three species are morphologically similar, with large decurrent leaf blades and accrescent fruiting calyces. *Solanum reflexiflorum* was not treated by Whalen (1984) or Nee (1999), and Agra (2007) left it unplaced. This species, endemic to the state of Bahia, Brazil, has reduced inflorescences, small flowers with reflexed calyx lobes, and glabrous fruits, but is evidently a member of the Erythrotrichum clade according to molecular data.

Thomasiifolium clade. — The Thomasiifolium clade is difficult to define morphologically, as it contains two seemingly distinct groups, both found in eastern Brazil. These include the shrubby to scandent *S. thomasiifolium* and *S. buddleifolium*, and the vines *S. paraibanum* and *S. rupincola*. All have plurifoliate sympodial units and pale lilac to blue or violet flowers with somewhat coriaceous corollas. The latter two climb using recurved prickles and have large, densely pubescent fruits with large seeds. The shrubs *S. thomasiifolium* and *S. buddleifolium* have straight spines and smaller, glabrous fruits with smaller seeds.

The Thomasiifolium clade includes species from Whalen's (1984) *S. polytrichum* species group (*S. rupincola*), taxa he left unplaced (*S. buddleifolium*, *S. thomasiifolium*), and *S. paraibanum*, which was described after his conspectus was published (Agra, 1992). Nee (1999) placed *S. buddleifolium* in sect. *Persicariae*, *S. paraibanum* in sect. *Micracantha*, and did not treat *S. rupincola*. He tentatively placed *S. thomasiifolium* in both sections *Erythrotrichum* and *Persicariae* because it shares morphological characteristics of both sections.

We have chosen to separate the Thomasiifolium clade from its sister group, the Erythrotrichum clade, due to its moderate support as a monophyletic and morphologically distinct group. This clade is in need of more morphological and molecular study and additional field work, and further study may show that it should be broken into two or more discrete clades.

Gardneri clade. — Members of the Gardneri clade are native from eastern to central Brazil (*S. agrarium*, *S. gardneri*, *S. polytrichum*, *S. stenandrum*) or the Caribbean (*S. microphyllum*, *S. schomburghii*, *S. tetramerum*) with one species from northern Peru (*S. talarense*). Defining the Gardneri clade morphologically is difficult. Possible uniting characteristics include a slender-stemmed, herbaceous to shrubby habit, straight, often needle-like prickles, small leaves in many species, short, laterally directed inflorescences, somewhat accrescent fruiting calyces, and preferences for arid habitats.

Species in the Gardneri clade come from multiple groups of previous classifications. Whalen (1984) left *S. gardneri*, *S. microphyllum*, and *S. tetramerum* (as the synonym *S. aquartia* Dunal) as unplaced species, although he noted that the latter two were probably related to each other. He placed *S. polytrichum* in the *S. polytrichum* species group, *S. stenandrum* and *S. agrarium* in the *S. mammosum* species group, and did not treat *S. schomburghii* or *S. talarense*. Nee (1999) also placed the species in disparate groups, with *S. gardneri*, *S. microphyllum*, *S. schomburghii*, and *S. tetramerum* (as *S. aculeatum* (Jacq.) O.E. Schulz) in sect. *Persicariae*, *S. polytrichum* in sect. *Polytrichum*, and *S. stenandrum*, *S. agrarium*, and *S. talarense* in sect. *Acanthophora*. The Gardneri clade also includes an undescribed species from Brazil.

Extensive sampling of Whalen's (1984) *S. mammosum* species group and Nee's (1999) sect. *Acanthophora* by Levin & al. (2005) revealed that *S. stenandrum* and *S. agrarium* lie outside the Acanthophora clade, despite the presence of mainly simple hairs on the adaxial leaf surfaces, a hallmark of the group. Levin & al. (2006) obtained this same result in their broader study of the spiny solanums; *S. stenandrum* and *S. agrarium* did not belong to the Acanthophora clade, but instead formed a well-supported group with *S. microphyllum* that was included as part of their Robustum clade. With our increased taxonomic sampling, we now recognize three clades, the Erythrotrichum, Thomasiifolium, and Gardneri clades, within the Robustum clade of Levin & al. (2006).

Solanum stenandrum and *S. agrarium* are morphologically similar to *S. talarense* from northern Peru and an undescribed species from the planalto of central Brazil. All share exclusively or predominantly simple and often glandular pubescence on the adaxial leaf surfaces, small leaves, and few-flowered inflorescences with white or greenish yellow corollas. All except *S. stenandrum* have a largely prostrate growth habit and all four species are adapted to arid habitats.

The remaining species of the Gardneri clade are a somewhat heterogeneous assemblage. Two species, *S. microphyllum* and *S. tetramerum*, have similar morphologies, including densely pubescent, reduced leaves, likely due to their similar habitats in xeric areas of the Caribbean. *Solanum schomburghii* and *S. gardneri* have similar appearances due to their dense, white stellate hairs and very long, tapering anthers. Finally, *S. polytrichum* is very distinctive due to its long, bristly pubescence and the prickly calyces that nearly completely cover the fruit. More sampling from eastern Brazil and the Caribbean will improve our phylogenetic understanding of the Gardneri clade. However, current results are sufficient to state that neither sect. *Polytrichum* nor sect. *Persicariae* as circumscribed by Nee (1999) are monophyletic.

Taxa unassigned among the 14 clades. — Despite broader sampling, four taxa, *S. campechiense*, *S. crotonoides*, *S. hieronymi*, and *S. multispinum* remain unassigned among the 14 clades recognized here. These are all taxa that also were unplaced in Levin & al. (2006). *Solanum campechiense*, a species from marshy areas of Central America, the Caribbean, and northeastern South America, continues to be an enigmatic species. Its sequences are highly divergent and it has

distinctive morphological characteristics including a sprawling habit, abundant straight prickles, deeply lobed leaves, and green, yellow, or purplish fruits surrounded by accrescent spiny calyces. Both Nee (1999) and Whalen (1984) suggested a relationship between *S. campechiense* and *S. sisymbriifolium*, but this relationship is not supported by our data. *Solanum crotonoides* is known only from montane forests of Hispaniola and is unusual in the spiny solanums in its dioecious reproductive system and strongly discolorous leaves due to almost lepidote pubescence on the abaxial surfaces. Nee (1999) placed *S. crotonoides* in sect. *Persicariae*, which is clearly not monophyletic (see discussion under Gardneri clade). Whalen (1984) placed *S. crotonoides* in the *S. crotonoides* species group along with three other species from the Caribbean, none of which were sampled in this study. Sampling these and other Caribbean species is key for understanding its phylogenetic affinities. As in Levin & al. (2006), *S. hieronymi* is supported as sister to the Elaeagnifolium + Old World clades. It is found in Argentina, Bolivia, and Paraguay and has morphological similarities with the Elaeagnifolium clade, including a rhizomatous, herbaceous habit, needle-like spines, and a densely, spiny accrescent calyx. Finally, *S. multispinum* also remains unplaced. It is found in Argentina, Paraguay, and adjacent regions of Brazil and is a small, rhizomatous herb with abundant needle-like prickles, an andromonoecious reproductive system, and mottled, yellow-green fruits. Its morphology and distribution point to it being related to members of the Carolinense clade; however, molecular data are, at present, inconclusive as to its relationships.

Steps to a systematic revision of the "spiny solanums". — A major contribution of this study is the identification of 14 major well-supported clades within the spiny solanums, using many New World taxa sampled here for the first time. In many cases, these clades are defined by unique morphological features and/or geographical ranges. Future studies are underway to resolve some of the remaining polytomies and ambiguously placed taxa using newly developed COSII markers (Wu & al., 2006; Rodriguez & al., 2009) and additional chloroplast markers (Shaw & al., 2007; Miller & al., 2009). Further taxonomic sampling, particularly from Brazilian and Caribbean species, is likely to identify new clades within the spiny solanums and clarify relationships within the Asterophorum, Gardneri, Thomasiifolium, and Erythrotrichum clades. More detailed studies of specific clades, particularly the Old World clade and *S. crinitum* species group, are in progress using much greater sampling density than that reported here. These molecular analyses, in concert with morphological studies, should lead us in the near future to a detailed understanding of evolutionary relationships in the large, complex, and widely distributed Leptostemonum clade.

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Appendix. Summary of species, collection location, vouchers, herbarium acronym, and GenBank accession numbers for taxa used in this study provided in the order ITS, *waxy*, and *trnT-F*. Dashed lines indicate that the region was not sampled for this accession. NIJ accession numbers refer to the Solanaceae collection at Radboud University, Nijmegen, the Netherlands. BIRM samples have the seed accession number for the Solanaceae collection at the University of Birmingham, U.K.

Solanum absconditum Agra, Brazil, *Agra & al. 7021* (JPB); GU591053, GU591105, GU590994. ***S. abutiloides*** (Griseb.) Bitter & Lillo, BIRM S.0655, *Olmstead S-73* (WTU); AF244716, AY562948, AY266236. **S. *acerescens*** Standl. & C.V. Morton, Costa Rica, *Bohs 2556* (UT); AY996480, AY996375, DQ180473. ***S. acerifolium*** Dunal, Costa Rica, *Bohs 2714* (UT); AY561261, AY562949, AY266149. ***S. acutilobum*** Dunal, Bolivia, *Bohs 2897* (UT); GU591054, GU591106, GU590995. ***S. adhaerens*** Roem. & Schult., Costa Rica, *Bohs 2473* (UT); AF244723, AY996377, DQ180474. ***S. aethiopicum*** L., BIRM S.0344, *Olmstead S-74* (WTU); AY996482, AY996378, DQ180394. ***S. agrarium*** Sendtn., Brazil, *Agra & al. 7027* (JPB); GU591055, GU591107, GU590996. ***S. albidum*** Dunal, Bolivia, *Nee 51831* (NY); GU591056, GU591108, GU590997. ***S. alternatopinnatum*** Steud., Brazil, *Agra & al. 7227* (JPB); HQ457395, HQ457414, HQ457404. ***S. arachnidanthum*** Rusby, Bolivia, *McClelland & Stern 412* (NY); GU591057, GU591109, GU590998. ***S. arboreum*** Dunal, Costa Rica, *Bohs 2521* (UT); AF244719, AY996381, DQ180424. ***S. argentinum*** Bitter & Lillo, Argentina, seeds from *Zygadlo 100. Bohs 2539* (UT); AF244718, AY996382, DQ180425. ***S. aridum*** Morong, Bolivia, *Bohs & Nee 2733* (UT); AY996499, AY996400, DQ180479. ***S. asperolanatum*** Ruiz & Pav., Bolivia, *Nee 51761* (UT); GU591058, GU591110, GU590999. ***S. asterophorum*** Mart., Brazil, *Agra & al. 7010* (JPB); GU591059, GU591111, GU591000. ***S. asteropilodes*** Bitter, Ecuador, *Bohs 3445* (UT); GU591060, GU591112, GU591001. ***S. aturense*** Dunal, Costa Rica, *Bohs 2976* (UT); AY996486, AY996385, GU591002. ***S. bahamense*** L., NIJ 944750187, *Bohs 2936* (UT); AY996487, AY996386, GQ149730. ***S. betaceum*** Cav., Bolivia, *Bohs 2468* (UT); AF244713, AY996387, DQ180426. ***S. bolivianum*** Britton, Bolivia, *Nee 51814* (NY); GU591061, GU591113, GU591003. ***S. bonariense*** L., Argentina, *Barboza & al. 1567* (CORD); GU591062, GU591114, GU591004. ***S. buddleifolium*** Sendtn., Brazil, *Agra 7164* (JPB); GU591063, GU591115, GU591005. ***S. campechiense*** L., Costa Rica, *Bohs 2536* (UT); AF244728, AY996389, DQ180475. ***S. candidum*** Lindl., Costa Rica, *Bohs 2898* (UT); AF244722, AY562953, AY266237. ***S. caricaefolium*** Rusby, Bolivia, *Bohs 2741* (UT); GU591064, GU591116, GU591006. ***S. carolinense*** L., BIRM S.1816, *Olmstead S-77* (WTU); AY996491, AY996392, DQ180476. ***S.* cf. Mentz sp. 1**, Brazil, *Agra & al. 7274* (JPB); HQ457403, HQ457422, HQ457413. ***S. chrysotrichum*** Schltdl., Costa Rica, *Soto & al. 1222* (UT); GU591065, GU591117, GU591007. ***S. cinereum*** R. Br., NIJ 904750120, *Bohs 2852* (UT); AY996493, AY996394, DQ180397. ***S. citrullifolium*** A. Braun, Texas, *Urbatsch 4834* (NY); GQ143647, GQ143679, GQ149732. ***S. comarapanum*** M. Nee, Bolivia, *Nee 51861* (NY); GU591066, GU591118, GU591008. ***S. comptum*** C.V. Morton, Paraguay, *Bohs 3193* (UT); AY996498, AY996399, GU591009. ***S. cordovense*** Sessé & Moç, Costa Rica, *Bohs 2693* (UT); AF244717, AY996401, DQ180480. ***S. coriaceum*** Dunal, NIJ A44750296, *Stern 425* (UT); GU591067, GU591119, GU591010. ***S. crinitipes*** Dunal, Colombia, *Olmstead S-81* (WTU); AY996500, AY996402, DQ180481. ***S. crinitum*** Lam., Brazil, *Agra & al. 7028* (JPB); GQ143651, GQ143683, GQ149736. ***S. crotonoides*** Lam., Dominican Republic, *Nee 52298* (NY); AY996502, AY996404, GU591011. ***S. decompositiflorum*** Sendtn., Brazil, *Agra & al. 7206* (JPB); GU591068, GU591120, GU591012. ***S. decorum*** Sendtn., Brazil, *Agra & al. 7263* (JPB); HQ457396, HQ457415, HQ457405. ***S. diploconos*** (Mart.) Bohs, Brazil, *Bohs 2335* (UT); AY523890, AY996407, DQ180429. ***S. donianum*** Walp., Mexico, *Bohs 3472* (UT); GU591069, GU591121, GU591013. ***S. dulcamara*** L., Cult. Michigan USA, no voucher; AF244742, AY996410, AY226231. ***S. elaeagnifolium*** Cav., Paraguay, *Bohs 3204* (UT); AY996508, AY996412, DQ180399. Texas, *Olmstead S-82* (WTU); AF244730, AY996413, GU591014. ***S. ensifolium*** Dunal, Puerto Rico, *Bohs 2461* (UT); AY996506, AY996409, DQ180483. ***S. furfuraceum*** R. Br., BIRM S.1442, *Olmstead S-84* (WTU); AY996512, AY996417, DQ180401. ***S. gardneri*** Sendtn., Brazil, *Agra & al. 7195* (JPB); GU591070, GU591122, GU591015. ***S. glaucophyllum*** Desf., No voucher; AF244714, AY996418, DQ180430. ***S. glutinosum*** Dunal, NIJ A34750191, *Bohs 3262* (UT); AY996513, AY996419, GU591016. ***S. grayi*** Rose, Mexico, *Vallejo-Marin 07s195* (MEX); GQ143659, GQ143690, GQ149744. ***S. hasslerianum*** Chodat, Argentina, *Barboza & al. 2121* (CORD); GU591071, GU591123, GU591071. ***S. hexandrum*** Vell., Brazil, *Agra & al. 7104* (JPB); GU591072, GU591124, GU591018. ***S. hieronymi*** Kuntze, Argentina, *Nee & Bohs 50761* (NY); AY996517, AY996423, GU591019. ***S. hindsianum*** Benth., Mexico, *Bohs 2975* (UT); AY996518, AY996424, DQ180402. ***S. hirtum*** Vahl, Ecuador, *Whalen 730* (QCA); AY263462, AY996425, AY266254. ***S. hoehnei*** C.V. Morton, Brazil, *Folli 1668* (MO); AY996519, AY996426, DQ180484. ***S. jabrense*** Agra & M. Nee, Brazil, *Agra & al. 7016* (JPB);

Appendix. Continued.

GU591073, GU591125, GU591020. ***S. jamaicense*** Mill., BIRM S.1209, *Olmstead S-85* (WTU); AF244724, AY562956, DQ180485. ***S. juvenale*** Thell., Argentina, *Barboza & al. 2071* (CORD); GU591074, GU591126, GU591021. ***S. laciniatum*** Aiton, New Zealand, *Bohs 2528* (UT); AF244744, AY996431, DQ180467. ***S. lanceifolium*** Jacq., Mexico, *Aguilar & al. 1130* (MO); GU591075, GU591127, GU591022. ***S. lanceolatum*** Cav., Costa Rica, *Bohs 2728* (UT); AY996523, AY996432, GU591023. ***S. lasiocarpum*** Dunal, Thailand, *Heiser 8008* (IND); AY263457, –,–. *Ansyar 9605* (IND) –, AY996433, AY266256. ***S. leucopogon*** Huber, Peru, *Stern & al. 152* (UT); GU591076, GU591128, GU591024. ***S. lycocarpum*** A. St.-Hil., Paraguay, *Bohs 3212* (UT); AY996525, AY996435, DQ812107. ***S. megalonyx*** Sendtn., Brazil, *Agra & al. 7090* (JPB); GU591077, GU591129, GU591025. ***S. melongena*** L., BIRM S.0657, *Olmstead S-91* (WTU); GU591078, AY562959, DQ180406. ***S. metrobotryon*** Dunal, Brazil, *Agra & al. 7275* (JPB); HQ457397, HQ457416, HQ457406. ***S. microphyllum*** (Lam.) Dunal, Dominican Republic, *Nee 52300* (NY); AY996529, AY996441, GU591026. ***S. mitlense*** Dunal, Mexico, *Whalen & Velasco 825* (BH); AY996530, AY996442, DQ812108. ***S. monachophyllum*** Dunal, Guyana, *Stern 256* (UT); GU591079, GU591130, GU591027. ***S. mortonii*** Hunz., Argentina, *Barboza & al. 639* (CORD); GU591080, GU591131, GU591028. ***S. moxosense*** M. Nee, Bolivia, *McClelland & Stern 408* (NY); GU591081, GU591132, GU591029. ***S. multispinum*** N.E. Br., Paraguay, *Bohs 3198* (UT); AY996533, AY996444, GU591030. ***S. nemorense*** Dunal, Bolivia, *Bohs & Nee 2757* (UT); AY996536, AY996447, DQ180488. ***S. palinacanthum*** Dunal, Bolivia, *Bohs 3151* (UT); AY561268, AY562961, AY266233. ***S. paludosum*** Moric., Brazil, *Agra & al. 7003* (JPB); GU591082, GU591133, GU591031. ***S. paniculatum*** L., Paraguay, *Bohs 3181* (UT); AY996540, AY996452, GU591032. ***S. paraibanum*** Agra, Brazil, *Agra & al. 7008* (JPB); GU591083, GU591134, GU591033. ***S. pedemontanum*** M. Nee, Ecuador, *Bohs 3337* (UT); GU591084, GU591135, GU591034. ***S. piluliferum*** Dunal, Brazil, *Agra & al. 7295* (JPB); HQ457398, HQ457417, HQ457407. ***S. pluviale*** Standl., Costa Rica, *Soto & al. 1225* (UT); GU591085, GU591136, GU591035. ***S. poinsettiifolium*** Rusby, Bolivia, *McClelland & Stern 414* (NY); GU591086, GU591137, GU591036. ***S. polytrichum*** Moric., Brazil, *Agra & al. 7099* (JPB); GU591087, GU591138, GU591037. ***S. pseudocapsicum*** L., BIRM S.0870, no voucher; AF244720, AY562963, DQ180436. ***S. ptychanthum*** Dunal, Chicago, *Olmstead S-94* (WTU); AF244735, AY996457, DQ180454. ***S. reflexiflorum*** Moric. ex Dunal, Brazil, *Agra 7182* (JPB); GU591088, GU591139, GU591038. ***S. refractum*** Hook. & Arn., Mexico, *Iltis & al. 29694* (WIS); AY996547, AY996460, HQ457408. ***S. rhytidoandrum*** Sendtn., Argentina, *Nee & Bohs 50861* (NY); GU591089, GU591140, GU591039. ***S. robustum*** H.L. Wendl., Argentina, *Bohs 3084* (UT); AY561270, AY562966, AY266259. ***S. rostratum*** Dunal, NIJ 934750126, *Cipollini 173* (UT); GQ143670, GQ143702, GQ149755. ***S. rudepannum*** Dunal, Costa Rica, *Soto & al. 1223* (UT); GU591090, GU591141, GU591040. ***S. rupincola*** Sendtn., Brazil, *Thomas & al. 1571* (MO); GU591091, GU591142, GU591041. ***S. schomburghii*** Sendtn., Suriname, *Clarke 11269* (US); GU591092, GU591143, GU591042. ***S. scuticum*** M. Nee, Brazil, *Agra & al. 7242* (JPB); HQ457400, HQ457419, HQ457410. ***S. sendtnerianum*** Van Huerck & Müll. Arg., Brazil, *da Cunha & Wang 310* (MO); GQ143671, GQ143703, GQ149756. ***S. sisymbriifolium*** Lam., Argentina, *Bohs 2533* (UT); AY561271, AY562967, AY266235. ***Solanum* sp. nov. Brazil,** Brazil, *Agra & al. 7108* (JPB); HQ457399, HQ457418, HQ457409. ***S. stagnale*** Moric., Brazil, *Bohs 3094* (UT); GU591093, GU591144, GU591043. ***S. stellativelutinum*** Bitter, Bolivia, *Wood & al. 18688* (NY); GU591094, GU591145, GU591044. ***S. stenandrum*** Sendtn., Brazil, *Irwin & al. 33085* (WIS); AY561273, AY562969, AY559242. ***S. stramoniifolium*** Jacq., Peru, *Whalen 860* (HUT); AY263465, AY562970, AY266263. ***S. subinerme*** Jacq., Panama, *Ebinger 321* (US); GU591095, GU591146, GU591045. ***S. subumbellatum*** Vell., Brazil, *Agra & al.* 7260 (JPB); HQ457401, HQ457420, HQ457411. S. ***talarense*** Svenson, Peru, *Sagastegui & Leiva 15487* (NY); GU591096, GU591147, GU591046. ***S. tampicense*** Dunal, U.S.A., no voucher; GU591097, GU591148, GU591047. ***S. tetramerum*** Dunal, Dominican Republic, *Garcia & al. 5909* (MO); GU591098, GU591149, GU591048. ***S. thomasiifolium*** Sendtn., Brazil, *Tavares & al. 5909* (MO); GU591099, GU591150, GU591049. ***S. torvum*** Sw., BIRM S.0839, *Olmstead S-101* (WTU); GU591100, AY562972, AY266246. ***S. tridynamum*** Dunal, BIRM S.1831, *Olmstead S-102* (WTU); GU591101, AY996474, DQ180412. ***S. ursinum*** Rusby, Bolivia, *Nee 51767* (NY); GU591102, GU591151, GU591050. ***S. urticans*** Dunal, Bolivia, *Bohs 2759* (UT); GU591103, GU591152, GU591051. ***S. vaillantii*** Dunal, Brazil, *Agra & al. 7238* (JPB); HQ457402, HQ457421, HQ457412. ***S. viarum*** Dunal, NIJ 934750190, *Cipollini 67* (UT); AY561275, AY562973, AY559243. ***S. wendlandii*** Hook. f., BIRM S.0488, no voucher; AF244731, AY562974, DQ180440. ***S. whalenii*** M. Nee, Bolivia, *Nee 51765* (UT); GU591104, GU591153, GU591052. ***S. wrightii*** Benth., Costa Rica, *Bohs 2445* (UT); GQ480731, GQ480733, GQ480732.

CHAPTER 4

A REVISION OF *SOLANUM* SECTION *ERIOPHYLLUM*

Abstract

Solanum sect. *Eriophyllum* (Solanaceae) includes 12 species native to the Caribbean, Central and South America. Section *Eriophyllum* is found within the large Leptostemonum clade, also known as the "spiny solanums" due to their sharp epidermal prickles. Plants of this section were historically placed in *Solanum* sect. *Micracantha*; however, the type species of that section, *S. micracanthos*, is a member of another section. Species in sect. *Eriophyllum* are scandent shrubs or vines with recurved spines, typically unbranched inflorescences, and deeply stellate corollas with strap-shaped lobes and very little interpetalar tissue. Within the Leptostemonum clade, sect. *Eriophyllum* is sister to the Bahamense clade from which it differs by its viny habit, recurved prickles, lack of strongly recurved fruiting pedicels and lack of stellate hairs on the adaxial surface of the anthers. The morphology, taxonomic history, nomenclature, ecology, distribution, reproductive biology, and phylogeny of *Solanum* sect. *Eriophyllum* are reviewed. Dichotomous and synoptic keys are provided for the species of the section.

Introduction

Solanum (Solanaceae) contains approximately 1400 species and is one of the 10 largest genera of flowering plants (Frodin 2004; Bohs 2005). Due to the large size and the morphological complexity of the genus, many infrageneric groups within *Solanum* are

not well understood, despite recent species level taxonomy (Knapp et al. 2004; http://www.nhm.ac.uk/solanaceaesource/). One of the largest clades within the genus is the Leptostemonum clade with approximately 350-450 species (Bohs 2005; Levin et al. 2006; Weese and Bohs 2007; Stern et al. 2011). This clade is characterized by the presence of stellate hairs and prickles, leading to the common name of "spiny solanums." The present study is a revision of *Solanum* sect. *Eriophyllum* Dunal, a group of 12 species within the Leptostemonum clade. The species in sect. *Eriophyllum* have traditionally been placed in various sections, most commonly in sect. *Micracantha* Dunal (Dunal 1813, 1816, 1852; Whalen 1984; Nee 1999); however, the type species for sect. *Micracantha*, *S. micracanthos* Lam., is a synonym of *S. subinerme* Jacq. Molecular data show that *S. subinerme* belongs to the Torva clade (hence sect. Torva) and is not a member of sect. *Micracantha* (Stern et al. 2011). *Solanum jamaicense* Mill. belongs to the Micracantha clade (Levin et al. 2006; Stern et al. 2011) and is the type species for sect. *Eriophyllum*. Thus, sect. *Eriophyllum* is the accepted name.

Solanum sect. *Eriophyllum* contains 12 species native to the Neotropics from southern Florida, the Caribbean, Mexico and Central America, to tropical South America. The species are all scandent shrubs or vines with porrect-stellate pubescence, difoliate sympodial units, extra-axillary unbranched inflorescences (except in *S. asperrimum*), and deeply divided stellate corollas.

Materials and Methods

The taxonomic conclusions in this study are based on observations of specimens in the herbarium and in the field, and are supported by molecular phylogenetic studies. I have examined specimens from the following herbaria: B, BM, BR, COCH, COL, CR, F,

FLAS, G, GH, GOET, INB, JPB, K, M, MO, NY, QCA, QCNE, QPLS, UC, US, USZ, UT, WIS, W. The authors have also collected eight species of sect. *Eriophyllum* in the field.

I have followed the morphological species concept in delimiting species of sect. *Eriophyllum*. Taxa are recognized as distinct if they possess a unique suite of characters and are separated from similar entities by morphological gaps. In nearly all cases, taxa also occupy geographically circumscribed ranges. Evidence from molecular data corroborated the delimitation of taxa using morphological methods and will be published elsewhere.

Measurements have been made from dried herbarium material supplemented by measurements from living material. Colors of corollas, fruits, etc., are described from living material or from herbarium label data.

Seed scanning electron microscopy (SEM) studies were performed by digesting seed coats using a 1% cellulase solution for 24 hours to remove the periclinal cell walls, exposing the anticlinal cell walls. For hair SEM studies, fresh stems were mounted on a stub with double-sided tape and coated with gold-palladium.

Plants used in pollination studies were grown from seed in the greenhouses at the University of Utah. Voucher information and original locality data are given in Appendix 1. For plants that were not autogamous, pollinations were effected by shaking pollen onto a glass slide that was rubbed against the stigma of the female plant. These were performed using flowers from the same individual (selfing) or using flowers from separate individuals or accessions (out-crossing). Success or failure of the pollination was monitored, as well as fruit size, shape, color, and number of seeds in successful crosses.

Sectional Delimitation and Relationships

All species of *Solanum* sect. *Eriophyllum* share the following combination of characters: 1) they are scandent shrubs or woody vines with recurved prickles; 2) mature, flowering portions of the stem have difoliate sympodial units; 3) the inflorescences are unbranched (except in *S. asperrimum*); 4) the corollas are deeply stellate with strap-shaped lobes and very little interpetalar tissue; 5) the fruits are glabrous and contain small seeds with a unique anticlinal wall arrangement. The monophyly of this section has also been confirmed using molecular data (Stern et al. 2011).

Solanum sect. *Eriophyllum* is morphologically similar to sect. *Torva* Nees. Most members of sect. *Torva* are large shrubs or small trees with straight prickles, that also have difoliate sympodial units. Most have many-branched inflorescences, and corollas with abundant interpetalar tissue. The seeds of species in sect. *Torva* are similar in size to those of sect. *Eriophyllum* but the latter has unique anticlinal cell walls. However, a few species, namely *S. poinsettifolium* Rusby, *S. subinerme* Jacq., and an undescribed species from northern Peru (annotated as "*S. junctum* M. Nee sp. nov. ined." on herbarium specimens), have convergent characteristics with sect. *Eriophyllum*. These species are scandent shrubs or vines and climb using recurved prickles. However, they have branched inflorescences and corollas with abundant interpetalar tissue.

Solanum sect. *Eriophyllum* is also similar to some members of *Solanum* sect. *Erythrotrichum* (Whalen) Child. Most members of sect. *Erythrotrichum* are large erect shrubs with reddish pubescence, plurifoliate sympodial units, unbranched or branched inflorescences, stelliform corollas with moderate interpetalar tissue, and pubescent fruits with large seeds (Whalen 1984).

Finally, members of sect. *Eriophyllum* are similar to two members of sect. *Crinitum* (Whalen) Child that are vining with recurved prickels, *S. coriaceum* Dunal and *S. sendtnerianum* Van Heurck & Müll.Arg. These species are unlike members of sect. *Eriophyllum* because they have large flowers with abundant interpetalar tissue, fruits with a swollen calyx, and large seeds that are characteristic of sect. *Crinitum*.

Taxonomic History

The first three species described in this group, *S. jamaicense* in 1768, *S. lanceifolium* in 1789, *and S. volubile* in 1797, made no mention of the alliances of these species with any other in the genus. It was not until 1813 that Michel Félix Dunal named both sects. *Eriophyllum* and *Micracantha*. The former contained *S. jamaicense* as well S. *brevipilum* Dunal*, S. heterotrichum* Dunal*,* and *S. cuneifolium* Dunal that are here recognized as synonyms of *S. jamaicense*. *Solanum jamaicense* is the only species from Dunal's sect. *Eriophyllum* from this or his later treatments that remains in the section in this study. The other four species he placed in sect. *Eriophyllum* were a heterogeneous mixture including *S. hirtum* Vahl (now in sect. *Lasiocarpa* (Dunal) D'Arcy), *S. tomentosum* L. and its synonym *S. coccineum* Jacq. (a member of the Old World clade), and *S. hybridum* Jacq. (a synonym of *S. aethiopicum* L. of the Old World clade). Dunal's sect. *Micracantha* contained *S. volubile, S. lanceifolium*, and *S. scabrum* (a synonym for *S. volubile*), which are all treated here, but also included a variety of species from what are now recognized as multiple groups. Dunal's 1816 description of *S. aturense* and *S. monachophyllum* added these two species to his sect. *Micracantha.* George Bentham described *S. flexicaule* in 1845 and placed it in sect. *Micracantha*. Dunal's 1852 circumscription of sect. *Micracantha* included this species and described *S. tampicense*.

In the 20th century, *S. leucopogon* was described by Otto Huber (Huber 1906) and was affiliated with *S. enoplocalyx* (a synonym of *S. volubile*). The description of *S. asperrimum* (Bitter and Moritz 1920) placed it within the large subgenus *Leptostemonum* but did not specify to which section it belonged. Neither the description of *S. arachnidanthum* (Rusby 1927) nor that of *S. apaporanum* (Schultes 1949) gave any indication of sectional relationships. Finally, the description of *S. pedemontanum* (Nee 2006) indicated that this species was similar to members of Whalen's (1984) *S. lanceifolium* species group and Nee's (1999) section *Micracantha*.

Whalen's (1984) circumscription of subgenus *Leptostemonum* divided the subgenus into 33 informally named species groups. His circumscription of the *S. lanceifolium* species group included 11 species, including *S. aturense, S. flexicaule, S. lanceifolium, S. leucopogon, S. tampicense* (as its synonym *S. houstonii*), and *S. volubile* (as its synonym *S. donnell-smithii*), that are included in the present definition of sect. *Eriophyllum*. Nee's (1999) treatment of *Solanum* species from the New World circumscribed sect. *Micracantha* to include 18 species, including *S. apaporanum, S. arachnidanthum, S. aturense, S. jamaicense, S. lanceifolium, S. leucopogon, S. monachophyllum, S. tampicense, S. volubile* (as its synonym *S. adhaerens*), and an undescribed species that would later be described as *S. pedemontanum* (Nee 2006). These species are treated here as sect. *Eriophyllum*; however, Nee's (1999) circumscription also included species that have been shown to belong to multiple other clades (Stern et al. 2011).

Whalen (1984) placed *S. subinerme* in his *S. subinerme* species group but placed *S. micracanthos* in his *S. lanceifolium* species group. Nee (1999) considered *S. micracanthos* a synonym of *S. subinerme*. He placed this species in sect. *Micracantha* but

made note that if it was actually more closely related to members of sect. *Torva*, then the name for sect. *Micracantha* would have to change. Dunal (1813) described sect. *Eriophyllum*, the original assemblage of which is now considered a heterogeneous group of species. D'Arcy (1972) lectotypified sect. *Eriophyllum* using *S. jamaicense* as the type species. This, combined with the later finding by Stern et al. (2011) that *S. subinerme* is a member of the Torva clade, makes sect. *Eriophyllum* the name for the species that have traditionally been placed in sect. *Micracantha*.

Morphology

Habit. Members of sect. *Eriophyllum* are erect to scandent shrubs or woody vines armed with recurved prickles. The armature of the species is somewhat correlated with the degree of climbing, as some of the weaker climbers, like *S. arachnidanthum* and *S. monachophyllum*, are more sparsely armed, while the stronger climbers, like *S. aturense* and *S. volubile,* are typically more densely armed. However, species like *S. tampicense*, which is a weak climber, can be extremely densely armed and form impenetrable thickets. *Solanum jamaicense* is the most erect species and often occurs as a shrub in pastures and cleared areas; however, even it is often scandent on fencerows or other vegetation. Three species, *S. arachnidanthum, S. monachophyllum,* and *S. tampicense,* are arching, festooning shrubs of seasonally inundated swamps and river banks. It is likely that *S. apaporanum* has a growth form similar to these species but it has not been observed by the authors and the original species description and label data typically refer to it as a "spiny shrub-vine." The remaining species, *S. aturense, S. lanceifolium, S. leucopogon, S. pedemontanum,* and *S. volubile*, are viny and strong climbers with the stems of *S. aturense* and *S. leucopogon* reaching 2-3 cm in diameter. The length of these

species is difficult to assess. Herbarium labels often place them in the 2-3 m range; however, field observations suggest that, although they are often collected at this height at forest edges, the true length of the stems can reach 20 m or more.

The flowering stems of all *Solanum* species exhibit sympodial growth (see Danert 1958, 1967, 1970: Child 1979; Bell and Dines 1995 for diagrams and explanations of terminology concerning sympoidal growth in *Solanum*). In this growth mode, the inflorescence terminates the shoot but growth is continued via an axillary lateral shoot. This axillary lateral shoot will in turn terminate in an inflorescence and growth will again be continued via an axillary lateral shoot. The number of leaves in each sympodial unit varies between species and groups within *Solanum*. Section *Eriophyllum* is characterized by difoliate sympodial units.

Trichomes. Trichomes can be found throughout the stems, leaves, and reproductive organs of species in sect. *Eriophyllum*. The majority of these trichomes are porrect-stellate hairs (Fig. 4.1) but occasional unbranched, multicellular, nonglandular or glandular hairs occur. The stems in sect. *Eriophyllum* are often densely pubescent, especially on younger growth, and the hair types can be diagnostic for some species. For example, the hairs of *S. leucopogon* are red with long midpoints (1-5 (8) mm while *S. aturense* and *S. volubile* have stem hairs that can be sessile or with greatly elongated stalks (1-4 mm) with a sessile midpoint, giving the hairs a bristly, umbrella-like appearance. While all species have at least some stellate hairs, the stems of *S. tampicense* and *S. arachnidanthum* are nearly glabrous with only occasional stellate hairs. The degree of pubescence is highly variable among collections of many species, particularly *S. aturense* and *S. volubile*, which is likely due to the age of the branch and the environmental conditions in which the plant was growing. With respect to age, the young

growth in species of sect. *Eriophyllum* is often densely pubescent wheras older stems can be nearly glabrous. Environmental conditions, such as the moisture regimen, amount of sun, and presence of predators, are also known to have an effect on the amount of pubescence within a species (Johnson 1975).

Leaves. Leaves in sect. *Eriophyllum* are all simple and may be unarmed or armed with recurved prickles along the midrib. Leaves in *S. arachnidanthum, S. tampicense,* and *S. volubile* are typically lobed while those of *S. jamaicense, S. leucopogon,* and *S. monachophyllum* are either entire or lobed. The leaves of *S. aturense* and *S. pedemontanum* are unlobed as are those of nearly all specimens of *S. lanceifolium* except a few aberrant collections from the Caribbean. The leaf bases are often strongly asymmetrical and are occasionally decurrent, especially in *S. jamaicense* where the petiole is often absent due to the decurrent base. In general, the petioles of species of sect. *Eriophyllum* are short (nearly absent to 2.5 cm) but may reach 4 cm in some species.

Inflorescences. The inflorescences of *Solanum* are morphologically terminal (see discussion of sympodial growth above), but with continuous growth the inflorescences in all species of sect. *Eriophyllum* appear to be extra-axillary. The inflorescences are unbranched, except in *S. asperrimum*, and are typically few-flowered (i.e., 2-15 flowers). Usually only one to three flowers per inflorescence are open simultaneously. The pedicels of all species are articulated at the base.

Flowers. The flowers of sect. *Eriophyllum* are typical of the genus in that they are pentamerous, perfect, and actinomorphic except in *S. tampicense* and occasionally *S. jamaicense*, which have deflected styles. The anthers are yellow and equal in length in all species and are strongly connivent in all species except *S. apaporanum*, *S. arachnidanthum*, *S. monahcophyllum*, and *S. tampicense*, which all spread outward to

some extent at maturity. The corollas of all species are stellate and lack interpetalar tissue. Flower color is typically white but in *S. asperimum*, *S. aturense*, and *S. volubile,* it ranges from white to purple. The ovaries range from glabrous to moderately pubescent with stellate or glandular hairs. The styles are all glabrous, although in species that have pubescent ovaries, some hairs may form on the lowermost portion of the style.

Fruits. Fruits in sect. *Eriophyllum* are either small (< 1.5 cm in diameter) and thin-skinned or larger (> 2.0 cm in diameter) with thicker, leathery skin. The small-fruited species include *S. apaporanum, S. arachnidanthum, S. jamaicense, S. monachophyllum,* and *S. tampicense*. *Solanum lanceifolium* and *S. asperrimum* have small berries but they are somewhat thicker skinned than the other small-fruited species. The large-fruited species include *S. aturense, S. leucopogon, S. pedemontanum*, and *S. volubile*. The fruits of *S. flexicaule* are intermediate in size (1-2 cm) and appear to be thin-skinned; however, this observation is based on a single fruiting herbarium specimen.

Regardless of size, fruits in the section are glabrous, although in some species the ovary is pubescent, specifically in *S. asperrimum, S. flexicaule*, and *S. volubile*, and some of these scattered hairs remain on immature fruits. The fruits are all green when immature and may be mottled, such as those of *S. jamaicense* which are mottled with light and dark green. All fruits mature orange to red. Seed dispersal has not been studied in sect. *Eriophyllum*, however, the brightly colored berries, sweet pulp, and small seeds suggest bird dispersal.

Seeds. Although the seeds of species in sect. *Eriophyllum* span a range of sizes, largely corresponding with fruit size, they are unique within the genus in having highly invaginated cell walls (Fig. 4.2). These walls are unlike any other members of closely related groups (Stern unpub. data).

Breeding Systems and Crossing Studies

Crossing experiments were performed in six species of sect. *Eriophyllum*. These include *S. aturense, S. jamaicense, S. leucopogon, S. pedemontanum, S. tampicense*, and *S. volubile* (see Appendix 1 for voucher information). These species had a variety of breeding strategies: plants of *S. jamaicense* and *S. tampicense* had only hermaphroditic flowers and were self-compatible. Plants of *S. aturense, S. leucopogon, S. pedemontanum,* and *S. volubile* were andromonoecious (see Walker and Whelen 1991 for terminology). Plants of *S. aturense* and *S.volubile* had some inflorescences with entirely male flowers and some inflorescences with entirely hermaphroditic flowers. These flowers can be distinguished by morphology, with functionally male flowers having a reduced gynoecia including a style that is not exserted beyond the stamens (Fig. 4.3). *Solanum aturense* and *S. volubile* required outcrossing to produce fruits. Sexual expression in *S. pedemontanum* and *S. leucopogon* varied with age. The first formed inflorescences are composed entirely of staminate flowers while inflorescences of older plants are composed of hermaphroditic flowers. A more descriptive term for these species might be "temporally andromonoecious." *Solanum pedemontanum* required outcrossing for fruit set while *S. leucopogon* had sporadic fruit set with selfing but much higher rates of fruit set with outcrossing. Field observation of *S. monachophyllum* and herbarium observation of *S. asperrimum* and *S. flexicaule* noted flowers with a functional style and some with a greatly reduced style, leading to the conclusion that these species are also andromonoecious.

Habitats and Distribution

Species of sect. *Eriophyllum* occur throughout the Neotropics, from ca. 26°N to nearly 17°S latitude. Species of the section occur in Mexico, all countries of Central America, throughout the Caribbean, and in northwestern South America south to Bolivia (Fig. 4.4). The greatest species diversity is in Central America and the Andes. Section *Eriophyllum* is not common in the Amazon Basin and nearly absent in eastern Brazil, except for the common tropical weed *S. jamaicense*.

The disturbed habitats that members of sect. *Eriophyllum* occupy are typical of the genus *Solanum*. Many species of *Solanum*, and particularly the spiny ones, are considered noxious weeds and thrive in forest gaps and edges, roadsides, and river banks (Nee 1979; Whalen 1984). These species have likely become more abundant as habitats have been increasingly disturbed by man (Knapp 2002). Species of sect. *Eriophyllum* likely require the high light intensity that these disturbed habitats provide. Species of the section are unlike other groups in *Solanum*, such as sects. *Torva* or *Crinitum*, in that they do not grow in dense stands and are typically not common where they occur (Whalen 1984).

Phylogenetic Relationships Within the Section

Members of the spiny solanums have been the subject of numerous molecular phylogenetic studies. The most extensive studies were those of Levin et al. (2006) and Stern et al. (2011); however, neither were able to resolve the placement of sect. *Eriophyllum* (as the Micracantha clade) within the spiny solanums. Stern and Bohs (in prep) expanded the number of molecular markers for representatives of various spiny solanum clades that were unresolved in previous studies, resulting in a well-resolved

phylogeny. This phylogeny places sect. *Eriophyllum* and places it sister to the Bahamense clade, a group of three species found in the Caribbean (Fig. 4.5). Section *Eriophyllum* differs from the Bahamense clade because the former has a viny habit, recurved prickles, and lacks strongly recurved fruiting pedicels and stellate hairs on the adaxial surface of the anthers (Strickland-Constable et al. 2010).

Molecular analysis sampling nine of the 12 species of sect. *Eriophyllum* found it to be monophyletic. The Bayesian posterior probabilities for relationships within the section are all 1.0; however, the higher-level relationships within the section have low bootstrap support values (< 50%-68%). The most strongly supported relationships in the phylogeny are those between species pairs, such as the placement of *S. volubile* sister to *S. aturense* and the placement of *S. arachnidanthum* sister to *S. tampicense*. These relationships will be discussed below.

Taxonomic Treatment

Solanum sect. *Eriophyllum* Dunal, Hist. Nat. Solanum 127, 189. 1813. Lectotype species: *S. jamaicense* Mill. (designated by D'Arcy 1972).

Erect to scandent shrubs or vines; stems and leaves nearly glabrous to densely pubescent with porrect-stellate trichomes. Sympodial units difoliate. Leaves simple, geminate, often slightly unequal in size. Inflorescence extra-axillary, unbranched (except in *S. asperrimum*), bearing 3->50 flowers (scars), but usually fewer than 10; pedicels articulated at the base. Flowers 5-merous, all perfect or a mixture of perfect and functionally male flowers due to a reduced style. Corollas stellate, deeply lobed, lacking interpetalar tissue. Anthers yellow, equal, attenuate, not opening into longitudinal slits with age. Fruit a berry, green when immature, maturing orange-red, glabrous or with a

few scattered porrect-stellate hairs. Seeds reniform, flattened, the surface cells netlike with pits separated by raised ridges.

Numerical List of Species

1. *S. apaporanum*
2. *S. arachnidanthum*
3. *S. asperrimum*
4. *S. aturense*
5. *S. flexicaule*
6. *S. jamaicense*
7. *S. lanceifolium*
8. *S. leucopogon*
9. *S. monachophyllum*
10. *S. pedemontanum*
11. *S. tampicense*
12. *S. volubile*

Synoptic List of Characters of Solanum Section Eriophyllum

Plants of Central America: 4, 6, 7, 11, 12

Plants of the Caribbean: 6, 7, 11, 12

Plants of the Guianas: 9, (12)

Plants of the Pantanal in Bolivia and Brazil: 2

Plants of the Amazon Basin: 1, 6, 9

Plants exclusively of riverbanks: 9

Leaves rhombic in outline: 6

Leaves lobed: 2, (7), 8, 9, 11, 12

Leaves subcoriaceous to coriaceous: 3, 4

Stems glabrous or nearly so: 2, 11

Stems with long-stalked stellate hairs (> 4 mm): 4, 12

Plants with red stellate hairs with a greatly elongated midpoint (>3 mm): 8

Abaxial leaf surface pale with stellate hairs: 10

Plants with small spines (typically < 1 mm): 5, 7

Inflorescence sessile or nearly so (peduncle < 3 mm): 6, 9, 11

Inflorescence branched: 3

Plants with anthers strongly spreading in flower: 2, 11

Fruits > 2 cm in diameter: 4, 8, 10, 12

Fruits < 1.5 cm in diameter: 1, 2, 6, 7, 9, 11

Seeds > 2.5 mm in diameter: 4

Key to the Species of Solanum Section Eriophyllum

1. Leaves rhombic in outline, strongly decurrent with petiole lacking; petals strongly reflexed; seeds minute, < 1 mm in diameter…. **6. *S. jamaicense*** Mill.

1'. Leaves not rhombic in outline, petioles evident; petals various; seeds > 1 mm in diameter … 2

2. Inflorescences branched 2-5 times… **3. *S. asperrimum*** Bitter & Moritz

2' Inflorescences unbranched… 3

3. Plant with lobed leaves … 4

3'. Plants with entire leaves… 9

4. Leaves deeply lobed (sinuses cut more than ¼ of the way to the midvein) …5

4’ Leave coarsely dentate, with small toothlike lobes (sinuses cut less than ¼ of the way to the midvein) … 7

5. Stems typically moderately to densely pubescent; hairs with elongated midpoint; fruits > 1.5 cm in diameter; plants of the eastern slope of the Andes… **8. *S. leucopogon*** Huber

5’. Stems nearly glabrous to sparsely pubescent; hairs lacking elongated midpoint; fruits <1 cm in diameter… 6

6. Flowers small, <8 mm in diameter; style deflected; young stems densely spiny; plants of Florida and Central America… **11. *S. tampicense*** Dunal

6’. Flowers large, > 1.5 cm in diameter; style not deflected; young stems sparsely to moderately spiny; plants of Northern Bolivia… **2. *S. arachnidanthum*** Rusby

7. Plants shrubby, only occasionally scandent; exclusively of riverside habitats; plants very sparsely spiny; leaves widest below midpoint; plants of Eastern Colombia, Venezuela, the Guyana Shield and Amazonian Brazil… **9. *S. monachophyllum*** Dunal

7’. Plants scandent, very viny; habitats various; plants moderately to densely spiny; leaves widest at midpoint; plants of Central America and Caribbean…8

8. Leaves typically < 8 cm long; moderately-densely pubescent below; pedicels threadlike at base and widening at juncture with fruit; spines equal in length, 1-2 mm long; flowers < 1 cm in diameter… **7. *S. lanceifolium*** Jacq.

8’. Leaves typically some leaves > 10 cm long; sparsely- moderately pubescent below; pedicels equally thick throughout; spines of various sizes, 2-8 mm long; flowers > 1.5 cm in diameter… **12. *S. volubile*** Sw.

9. Fruits 5-10 mm (12 mm) in diameter… 10

9’ Fruits usually (10) 15-30 mm in diameter…12

10. Stems and abaxial surface of leaves nearly glabrous to sparsely pubescent; leaves widest below midpoint with long acuminate tip; pedicels filiform (< 1mm wide), not expanding at apex; plants of riverine habitats Amazon lowlands (at base of Andes?) Brazil, Colombia, Ecuador, Peru… **1. *S. apaporanum*** R.E. Schultes

10’ Stems and abaxial surface of leaves moderately to densely pubescent; leaves widest at midpoint with acute to obtuse tip; pedicels filiform and expanding at apex or thick (> 1 mm wide) throughout; plants of Central America Caribbean and Guiana Shield… 11

11. Plants scandent to vines; pedicels threadlike at base and widening distally; plants moderately spiny with spines equal in length, 1-2 mm long; plants of Central America and Caribbean… **7. *S. lanceifolium*** Jacq.

11’ Plants shrubby, only occasionally scandent; pedicels equal throughout; plants very sparsely spiny with spines >2 mm long; plants of Eastern Colombia, Venezuela, the Guyana Shield and Amazonian Brazil… **9. *S. monachophyllum*** Dunal

12. Stellate hairs with elongate midpoints; calyx lobes acuminate… **8. *S. leucopogon*** Huber

12’ Stellate hairs brisltelike, lacking midpoint or with short midpoint but never with elongate midpoint; calyx lobes truncate to short lobed… 13

13. Stem pubescence sessile (or nearly so); abaxial surface of leaves pale with dense tomentum; plants Colombia, Ecuador, Peru, Boliva, Brazil… 14

13’ Stem pubescence short-stalked to bristle-like; abaxial surface of leave not pale; plants of Central America and the Caribbean…15

14. Abaxial surface of leaves pale with dense tomentum; corolla 2.5-5 cm in diameter; ovary glabrous or sparsely pubescent; plants of the eastern slopes of the Andes

into the Amazon in Colombia, Ecuador, Peru, Boliva, Brazil… **10. *S. pedemontanum*** M. Nee

14'. Abaxial surface of leaves dark green; corolla 1.5-2.5 cm in diameter; ovary densely pubescent; plants of western coast of Ecuador… **5. *S. flexicaule*** Benth.

15. Stem hairs often long-stalked, bristle-like; leaves subcoriaceous, somewhat lustrous, margin revolute; corollas 3-5 cm in diameter; anthers 10-14 mm long; ovaries, style, and young fruits glabrous; fruit 2-3 (5) cm in diameter; seeds 3.5-6 mm… **4. *S. aturense*** Dunal

15'. Stem hairs sessile or short-stalked, not bristle-like; leaves membranaceous, not lustrous, the margin not revolute; corollas 1.5-3 cm in diameter; ovaries, style, and young fruits stellate-pubescent; anthers 5-10 mm long fruit 1-1.5 cm in diameter; seeds 2-3 mm …. **12. *S. volubile*** Sw.

Solanum apaporanum (1) R. E. Schult., Bot. Mus. Leafl. 13: 292. 1949. — TYPE. COLOMBIA. Vaupes: Macaya-Ajaju River confluence, Mount Chiribiquete, quartzite base, summit 800-1200 ft. above forest floor, 1700-2100 ft. above sea level, 15-16 May 1943 (fl, fr), *Schultes 5406* (holotype: GH! [GH77576]; isotypes: COL! [COL000004229], K! [K000590288]).

Scandent shrub to vine 1-4 m. Stems sparsely armed with recurved, tan to brown roselike prickles, these 1-2 mm long, the base 0.5-1.5 x 0.2-0.6 mm, moderately pubescent with tan to rusty, porrect-stellate hairs, the stalks nearly absent to 0.5 mm, multiseriate, the rays 4-8, 0.5-1 mm, unicellular to multicellular, the midpoints nearly absent. Flowering portions of the stem consisting of difoliate sympodial units, the leaves geminate, those of a pair often unequal. Leaves simple, the blades 4-15 x 2-5 cm, ovate, unlobed, chartaceous, slightly discolorous, dark green adaxially, light green abaxially, the

adaxial surface moderately pubescent with stellate hairs like those of the stem but with the midpoints 0.5-1 mm long, the abaxial surface moderately to densely pubescent with hairs like those of the stem; major veins 4-6 on either side of the midvein, the secondary veins obscure, the midrib abaxially with a few recurved prickles like those of the stem; base obtuse, occasionally slightly asymmetrical; apex acute; petioles nearly absent to 1.5 cm, moderately pubescent with hairs like those of the stem, armed with a few prickles like those of the stem. Inflorescences 3-6 cm, extra-axillary, unbranched, with 4-10 flowers, apparently all perfect, the axes moderately pubescent with hairs like those of the stem, unarmed; peduncle nearly absent to 3 cm; rachis 2-5 cm; pedicels 3-10 mm in flower, 10-15 mm in fruit, filiform, contiguous to very slightly expanded at distal end, spaced 1-5 mm apart. Calyx 1-2 mm long, the tube 0.5-1mm, the lobes 0.5-1 x 0.25-0.5 mm, triangular, moderately pubescent with hairs like those of the stem, unarmed; fruiting calyx 2-3 mm, not accrescent in fruit. Corolla 7-13 mm in diameter, chartaceous, white, stellate, lobed nearly to the base, lacking interpetelar tissue, the lobes 3-6 x 0.75-1.5 mm, narrowly triangular, moderately pubescent abaxially with stellate hairs like those of the adaxial leaf surface, glabrous adaxially. Stamens 4-7 mm; filaments 1-2 mm, glabrous; anthers 4-6 x 0.8-1.4 mm, attenuate, tapering, connivent, yellow, the base cordate, the apex obtuse, the pores apical, directed slightly intorsely. Ovary glabrous; style 7-9 x 0.5-1 mm, exserted beyond the stamens, cylindrical, white, glabrous; stigma to 1 mm wide, cylindrical, green. Fruit a berry, 5-8 mm in diameter, globose, green with dark green mottling when immature, orange when mature, glabrous. Seeds 30 per fruit, 2-2.5 x 1.5-2 mm, reniform, brown, the surface netlike with pits separated by raised ridges (Fig. 4.6).

Habitat and distribution. (Fig. 4.7) Found in riverine habitats in the upper Amazon drainages of Brazil, Colombia, and Peru at 100-500 (750) m.

Etymology. The epithet refers to the type locality along the Río Apaporis in southeastern Colombia.

Notes. *Solanum apaporanum* is one of the few members of sect. *Eriophyllum* found in the Amazon Basin. The relatively few collections of this species indicate an extensive range throughout Amazonia. The type locality and many of the collections are from the area near the Parque Nacional Natural Sierra de Chiribiquete in southeastern Colombia with additional populations from the Iquitos, Peru and Manaus, Brazil areas. The latter two localities are the most heavily collected in the Amazon Basin and indicate that the species is likely more widespread but undercollected. The few, far-ranging collections make it difficult to assess morphological variability within this species.

Morphologically *S. apaporanum* is similar to *S. lanceifolium* in having small (1-2 mm) recurved prickles, small flowers (corollas 7-13 mm in diameter), entire leaves, and small fruits (5-8 mm in diameter). However, *S. apaporanum* differs in having leaves that are widest below the midpoint with a long acuminate tip, and filiform pedicels (< 1 mm wide) that do not expand at the distal end (Fig. 4.6).

Additional specimens examined. BRAZIL**. Amazonas:** Rio Negro, eastern margins of Anavilhanas Islands, ca 2°41'S, 60°19'W, 24 Jul 1991 (fl, fr), *Mori & Gracie 21850* (MO); Rio Negro, Santo Antonio, 2°25'S 60°58'W, 12 Jun 1990 (fl, fr), *Mori et al. 21291* (MO); South branch Rio Negro to its confluence with Rio Solimoes, May 1851 (fl, fr), *Spruce 1560* (BM, W).

COLOMBIA**. Amazonas:** Mun. de Leticia, Corregimiento de Tarapacá, Parque Nacional Natural Amacayacu, Cabaña Lorena (Inderena) y Caño Lorena, 3°01'S, 70°02'W, 100 m, 21 Jun 1991 (fr), *Rudas et al. 2252* (MO); Río Apaporis, entre el Río Pacoa y el Río Kananarí, Soratama, 250 m, 21 Jun 1951 (fl), *Schultes & Cabrera 12717*

(US); Amazonas-Vaupes, Río Apaporis, entre el Río Pacoa y el Río Kananari, Soratama, 250 m, 16 Aug 1951 (fl), *Schultes 13531* (COL); Amazonas-Vaupes, Río Apaporis, Jinogojé (at mouth of Río Piraparaná) and vicinity, about 700 ft, 0°15'S, 70°30'W, 8 Jun 1952 (fl), *Schultes & Cabrera 16681* (US); same loc., Mar 1952 (fr), *Schultes & Cabrera 19828* (US). **Vaupes:** Mitú and vicinity, along lower Río Kuduyarí, 1 Aug 1975 (fl, fr), *Zarucchi 1464* (K, MO).

PERU**. Loreto:** Río Nanay between Iquitos and Puerto Alemendrez, 120 m, 13 Jul 1976 (fr), *Gentry & Revilla 16713* (MO); along the Rio Nanay near the Boca toma of Iquitos, 15 Feb 1968 (fl, fr), *Simpson & Schunke 659* (G, US); Prov. Iquitos, Estacíon Biologica Quebrada Blanco, close to Rio Tahuayu (tributary of Rio Tamshiaco), 200 m, 11 Jul 1998 (fl, fr), *Skrabal & Franke 98/60* (M).

Solanum arachnidanthum (2) Rusby, Mem. New York Bot. Gard. 7: 345. 1927. — TYPE: BOLIVIA. Beni: Trinidad, 700 ft, Mar 1922, *M. Cardenas "3 special"* (lectotype, **here designated**: NY! [NY00139051]; isolectotype: NY! [NY00139052])

Shrub 1-3 m, occasionally scandent on other vegetation. Stems moderately armed with recurved tan to orange roselike prickles, these 2-6 mm long, the base 2-4 x 0.5-1.5 mm, nearly glabrous to sparsely pubescent with white to tan, porrect-stellate hairs, the stalks nearly absent to 0.5 mm, multiseriate, the rays 4-8, 0.5-1 mm, unicellular to multicellular, the midpoints nearly absent. Flowering portions of the stem consisting of difoliate sympodial units, the leaves geminate, those of a pair slightly unequal. Leaves simple, the blades 3-15 x 1-8 cm, ovate, chartaceous, slightly discolorous, dark green adaxially, green to whitish green abaxially, with both leaf surfaces sparsely to moderately pubescent with hairs like those of the stem but with the stalks absent and the midpoints 0.5-1 mm; major veins 3-5 on either side of the midvein, the secondary veins obscure, the

midrib abaxially with a few to many recurved prickles like those of the stem but 0.5-1 mm long; base acute, often asymmetrical; margin with 2-3 obtuse lobes per side, the sinuses cut less than 1/3 of the way to the midvein; apex acute; petioles 0.5-2 cm, sparsely to moderately pubescent with stellate hairs like those of the stem, sparsely to moderately armed with prickles like those of the stem but 1-2.5 mm long. Inflorescences 3-9 cm, extra-axillary, unbranched, with 3-8 (-13) flowers, apparently all perfect, the axes nearly glabrous to moderately pubescent with hairs like those of the stem, unarmed; peduncle nearly absent to 1.5 cm; rachis 1.5-8 cm; pedicels 5-10 mm in flower, 10-15 mm in fruit, filiform, slightly expanded distally, spaced 1-5 mm apart. Calyx 2-4 mm long, the tube 2-4 mm, the lobes absent to 0.5-1 x 0.25-0.5 mm, triangular with acute apices, sparsely to moderately pubescent with stellate hairs like those of the adaxial leaf surface, unarmed; fruiting calyx 3-5 mm, the lobes often reflexed, not accrescent in fruit. Corolla 2.5-3.5 cm in diameter, chartaceous, white, stellate, lobed nearly to the base, the lobes 13-17 x 1.5-2.5 mm, lanceolate, densely pubescent abaxially with hairs like those of the calyx, nearly glabrous adaxially. Stamens 13-17 mm; filaments 1-1.5 mm long, glabrous; anthers 12-16 x 0.75-1.25 mm, attenuate, tapering, connivent in bud, connivent to spreading in flower, curved upward at distal end, yellow, the base cordate, the apex obtuse, the pores apical, directed slightly introrsely. Ovary glabrous; style 20-25 x 0.5-1 mm, exserted beyond stamens, curved upward at distal end, cylindrical, white, glabrous; stigma 0.5-1 mm wide, green. Fruit a thin-skinned berry, 0.5-1 cm in diameter, globose, green when immature, orange-red when mature, glabrous. Seeds 30-40 per fruit, 1.5-2 x 1-1.5 mm, reniform, brown, flattened, the surface netlike with many pits separated by small raised ridges, the margin slightly swollen (Fig. 4.8).

Habitat and distribution. (Fig. 4.7) In seasonally flooded savannas of the Llanos de Moxos of Depts. Beni, Pando, and Santa Cruz, Bolivia, at 125-275 m in elevation.

Etymology. The name for this species is derived from the Greek "arachnid-" meaning "spider" and "-anthum" meaning "flower", referring to the long, thin corolla lobes and curving, spreading anthers.

Notes. *Solanum arachnidanthum* is somewhat geographically isolated within sect. *Eriophyllum* and occurs in the southernmost extent of the section's range in the Llanos de Moxos, a vast area of seasonally flooded savannas in the southwestern Amazon Basin in northern Bolivia and the adjacent Brazilian state of Rondônia. This seasonally flooded habitat is reminiscent of the periodically flooded swampy areas occupied by *S. tampicense*, a species found in Florida, the Caribbean, and Central America.

Solanum arachnidanthum is one of the most easily recognizable species in sect. *Eriophyllum*. It has a festooning growth form with slender stems that drape over other vegetation and vicious recurved prickles that latch on to other plants (Fig. 4.8). It is possible that it is spreads rhizomatously, as it forms dense stands where it occurs (Fig. 4.8a). The flowers are also distinct, with some of the longest anthers of the section (12-16 mm) that curve and spread upon anthesis (Fig. 4.8c).

Phylogenetic results strongly support (100% BS, 1.0 PP) the sister relationship of *S. arachnidanthum* and *S. tampicense* (Stern and Bohs in prep). Although the flowers of *S. arachnidanthum* are some of the largest in the section and those of *S. tampicense* are among the smallest, their festooning growth form, sparse pubescence, and small, thin-skinned fruits are very similar.

The original species description of *S. arachnidanthum* did not specify a herbarium or specific collection as the holotype, so one of the two NY specimens is designated here

as the lectotype. The specimens are similar, but the NY00139051 collection is a larger branch with more leaves, flowers, and fruits. The collection number was written as "3 special" by Cardenas and likely indicates that he acknowledged that this was an unknown species.

Additional specimens examined. BOLIVIA**. Beni:** Prov. Cercado, W side of Trinidad, 14°50'S, 64°55'W, 150 m, 22 Feb 1987 (fl, fr), *Nee 34260* (MO, US); Prov. Cercado, Trinidad, 14°50'S, 64°55'W, ca. 200 m, 6 Jan 1989 (fl), *Nee 37521* (MO); Prov. Cercado, 7 km SW of Trinidad, vic. Puerto Almacen, along the Rio Ibare, a tributary paralleling the Rio Mamore, 14°52'S, 64°57'W, ca. 200 m, 7 Jan 1989 (fl), *Nee 37551* (MO). **Pando:** Prov. Madre de Dios, along Rio Madre de Dios, Genechiquia, 11°17'S, 66°49'W, 125 m, 4 Sep 1985 (st), *Nee 31786* (MO); Prov. Madre de Dios, Laguna de Candelaria, an oxbow lake in the floodplain of the Rio Madre de Dios, 23 km (by air) WSW of Riberalta, 11°03'S, 66°17'W, 125 m, 20 Aug 1985 (st), *Nee & Moraes 31442* (MO, US). **Santa Cruz:** Prov. Sara, Municipio Santa Rosa del Sara, Laguna Juán Chulo, 16 km al NW de Santa Rosa del Sara, 17°00'S, 63°44.6'W, 250 m, 9-10 Mar 1996 (fl, fr), *Fuentes 1571* (MO); Prov. Nuflo de Chavez, Perseverancia, vecindad del Río Negro, tributario del Río Baures, a 75 km sur del limite del Dpto. de Beni y 150 km W del Río Paragua, 14°38'S, 62°37'W, 200 m, 17 May 1991 (fl, fr), *Mostacedo 118* (F); Prov. Guarayos [formerly part of Prov. Nuflo de Chavez], along Rio Negro, 2 km S (upstream) of Perseverancia, 14°45'S, 62°47'W, 275 m (st), *Nee 38800* (MO).

Solanum asperrimum (3) Bitter & Moritz, Repert. Spec. Nov. Regni Veg. 16: 393. 1920. —TYPE: VENEZEULA. Mérida, *J. Moritz 1024* (holotype, BM! [BM000513272]; isotypes, B, LE, MO! [MO-1625283], P; photo of B isotype [F neg. 2685: F!, G!]; photo of P isotype [F neg. 8148: F!])

Solanum secundum Bitter & Moritz, Repert. Spec Nov. Regni Veg. 16: 391. 1920. — TYPE: VENEZUELA. Edo. Aragua, Colonia Tovar, *J. Moritz 1906* (Holotype: BM! [BM000887998]; isotype W! [W0003294]).

Scrambling vine 1-6 m. Stems moderately armed with recurved tan to orange roselike prickles, these 1-4 mm long, the base 2-4 x 0.5-1 mm, moderately to densely pubescent with orane to red, porrect-stellate hairs, the stalks 0.5-1.5 mm, multiseriate, the rays 6-10, 0.5-1 mm, unicellular to multicellular, the midpoints under 0.5 mm in length, but forming a distinct swelling. Flowering portions of the stem consisting of difoliate sympodial units, the leaves geminate, those of a pair slightly unequal in size. Leaves simple, the blades 5-15 x 3-9 cm, ovate, subcoriaceous to coriaceous, slightly discolorous, dark green adaxially, green abaxially, adaxial leaf surfaces nearly glabrous to moderately pubescent with stellate hairs like those of the stem but with the stalk nearly absent and the midpoint 0.5-1 mm, abaxial leaf surface moderately to densely pubescent with stellate hairs like those of the stem; major veins 4-6 on either side of the midvein, the midrib abaxially moderately armed with recurved prickles like those of the stem but 0.5-1.5 mm long; base obtuse, often asymmetrical; margin entire, occasionally revolute; apex acute; petioles 1-3 cm, moderately pubescent with stellate hairs like those of the stem, sparsely to moderately armed with prickles like those of the stem. Inflorescences 8-15 cm, extra-axillary, occasionally unbranched but more commonly branched with up to 6-8 major branches, with 15-50 (or more) flowers, apparently andromonoecious, the axes moderately to densely pubescent with hairs like those of the stem, unarmed; peduncle 2-5 cm; rachis 4-9 cm; pedicels 3-10 mm in flower, 8-15 mm in fruit, filiform, spaced 1-3 mm apart. Calyx 1-3 mm long, the tube 1-2.5 mm, the lobes nearly absent to 0.5-1 x 0.25-0.5 mm, narrowly triangular, densely pubescent with stellare hairs like those of the

stem, unarmed to sparsely armed with straight, tan prickles 0.5-1 mm in length; fruiting calyx 3-6 mm, not accrescent in fruit. Corolla 2-3.5 cm in diameter, chartaceous, white to pale purple, stellate, lobed nearly to the base, the lobes 10-18 x 2-4 mm, narrowly triangular, densely pubescent abaxially with hairs like those of the calyx but with midpoint 0.5-1 mm in length, nearly glabrous adaxially, the adaxial midvein with occasional stellate hair like those of the abaxial surface. Stamens 10-15 mm; filaments 0.5-1 mm long, glabrous; anthers 10-15 x 1-1.5 mm, glabrous or occasionally with stellate hairs on outer surface, attenuate, tapering, connivent in bud, connivent to slightly spreading in flower, yellow, the base cordate, the apex obtuse, the pores apical, directed slightly introrsely. Ovary moderately to densely pubescent with stellate hairs like those of the corolla; style 4-7 x 0.5-1.0 mm, not exserted beyond stamens, style in hermaphroditic flowers 12-16 x 0.5-1.0 mm, exserted beyond stamens, cylindrical, in functionally male flowers 4-7 x 0.5-1.0 mm, not exseted beyond stamens, cylindrical, glabrous, style in hermaphroditic flowers 12-16 x 0.5-1.0 mm, exserted beyond stamens, cylindrical, white, pubescent proximally with stellate hairs like those of the ovary, glabrous distally; stigma 0.5-1mm wide, green. Fruit a leathery berry, 1-2 cm in diameter, globose, green when immature, orange-red when mature, glabrous. Seeds 40-80 per fruit, 1-1.5 x 0.75-1.0 mm, reniform, tan to brown, flattened (Fig. 4.9).

Habitat and distribution. (Fig. 4.10) Disturbed roadsides and forest edges in the eastern arm of the Andes in the Colombian departments of Boyaca, Santander, and Norte del Santander and throughout the mountains in the northwest of Venezuela at (100) 500-2600 m in elevation. It does not appear to enter the Maracaibo lowlands, the Gran Sabana, or the Guiana Shield.

Etymology. The name for the species is derived from the Latin "asperi-" meaning "rough", likely referring to the coriaceous leaves and dense pubecence found throughout the plant.

Notes. *Solanum asperrimum* can easily be distinguished because it is the only member of the section with branched inflorescences. In the past it has been treated as a synonym of *S. aturense*, likely due to the similar pubescence and leaves; however, the branched inflorescences, small fruits, and small seeds are unique to *S. asperimmum*. The geographic distributions of these species is also somewhat distinct, with *S. asperimmum* found in the eastern arm of the Andes in the far east of Colombia into Venezuela while *S. aturense* is distributed from Mexico through Central America to eastern Colombia.

Both the name *S. asperrimum* and *S. secundum* were published the in Bitter (1920). The quality of the type material for these two names is comparable and their distribution in various herbaria is similar. The name *S. asperrimum* was chosen because many specimens had previously been identified as this (although they were later changed to *S. aturense*) while the name *S. secundum* was rarely used.

Additional specimens examined. COLOMBIA**. Boyaca:** Region of Mt. Chapon, extreme western part of Dept. Boyaca, NW of Bogota, 3 Jul 1932 (fl), *Lawrance 290* (A, F, US). **Guajira:** 25 km SW of Carraipia, comisaria Guajira, 150 m, 26 Aug 1944 (fl), *Haught 4330* (F, US). **Norte del Santander:** Región del Sarare, entre el Alto del Loro y el Alto de Santa Inés, 1800-2200 m, 18-21 Oct 1941 (fl), *Cuatrecasas 12531* (F, GH, US); Región del sarare, hoya del Río Margua, en la Quebrada del Río Negro, 1200-1300 m, 9 Nov 1941 (fl), *Cuatrecasas 12918* (F, US); Between Pamplona and La Isla, 2000-2500, 27 Feb 1927 (fl), *Killip & Smith 19798* (A, GH, US); Loso and vicinity (north of Toledo), 2200-2400 m, 6-7 Mar 1927 (fl), *Killip & Smith 20475* (A, GH, US); Western

side of Culagá Valley, north of Labateca, 1480-1550 m, 12 Mar 1927 (fl), *Killip & Smith 20546* (US). **Santander:** Mesa de los Santos, 1500 m, 11-15 Dec 1926 (fl), *Killip & Smith 15071* (US); Campo Capote and vicinity, 100-200 m, 6°38’ N, 73°55’ W, 9 Jul 1971 (fl), *Nee & Mori 4316* (US); Quebrada la sorda (sabana de torres), 900 m, 12 Aug 1977 (fr), *Rentería et al. 531* (MO).

VENEZUELA**. Apure:** Dist. Páez, selva de Cutufí, between Cutufí on the Río Cutufí and the Río Sanare, 7°09-11’ N, 71°56-58’ W, 300-350 m, 8-12 Nov 1982 (fl), *Davidse & González 21876* (BM, MO). **Aragua:** Colonia Tovar, 1800-2000 m, Dec 1924 (fl), *Allart 314* (US); Tovar, 2000 m, 9 Aug 1957 (fl), *Bro. Antonio 432* (US); Alto de Choroní, 1450 m, 26 Oct 1940 (fl), *Chardon 178* (US); Along highway from Maracay to Choroni at or near Altos de Choroni, 9 Feb 1973 (fr), *Croat 21448* (MO); Colonia Tovar and vicinity, 1700-2300 m, 30 Dec 1921 (fl, fr), *Pittier 10054* (US); Parque Nacional Henry Pittier, between trail up Periquito and Fila de Periquito, along upper slopes of tributary to Quebrada Palo Vaco, on side towards Lago Valencia, opposite Rancho Grande Biological Station, 1300-1400, 25 Oct 1961 (fl), *Steyermark 89906* (US); Parque Nacional Pittier, Regresiva del Diablo, along road between El Castaño and Choroni, 1550 m, 21 Sep 1977 (fl), *Steyermark & Huber 114238* (MO). **Falcón:** Dist. Bolívar, Sierra de San Luis, Cerro Galicia, 11°11’ N, 69°42’ W, 1500 m, 29 Mar 1984 (fl), *Plowman et al. 13434* (F); Sierra de San Luis, entre La Chapa y Uria, 1400 m, 19 Jul 1967 (fl), *Steyermark 99204* (US). **Distrito Federal:** El Junquito, Sep 1969 (fl), *Aristeguieta 7320* (F, MO); El Junquito, lado que mira al mar entre El Junquito y Tibrón, propriedad de la finca agropecuaria Tibrón, 10°28’ N, 67°05’ W, 1830-1850 m, 19 May 1992 (fr), *Meier* 2277 (GH); 9 km W of El Junquito on road between Caracas and Colonia Tovar, ca. 1900 m, 26 Jul 1979 (fl), *Nee & Whalen* 16870 (F); same loc., (fl, fr), *Nee & Whalen* 16874

(F); A lo largo del camino entre “Portachuelo” y “Peñita” en las cabeceras del Río Chichiriviche, entre Geremba y Hacienda El Limón, 8-10 km abajo de Geremba, 1300-1500 m, 12 Feb 1966 (fr), *Steyermark 94758* (US); Agua Negra, 1200 m, 2 Jan 1940 (fr), *Williams 12465* (F, US). **Lara:** Dist. Iribarren, en la Fila de Las Goteras, arriba de las cabeceras del Río Claro, al sur de Río Claro, 1500-1550 m, 11 Aug 1970 (fr), *Steyermark et al. 103728* (US). **Mérida:** La India, 1650-2350 m, 17 Feb 1957 (fl), *Bernardi 6231* (G); La Carbonera, 2300-2500 m, 6 Nov 1976 (fl, fr), *Bernardi et al. 17201* (G); Dist. Andrés Bello, Quebrada La Lajita, ca. 4 km N of La Azulita by road, 8°43’ N, 71°26’ W, 800 m, 1 Jul 1980 (fl), *Davidse & González 18858* (MO); Prope coloniam Tovar, 1854-1855 (fl), *Fendler 995* (GH, K, MO); same loc., (fl, fr), *Fendler 997* (GH); Dist. Briceño, “El Calvario”, Palmira, 1350 m, 12 Oct 1973 (fr), *Lopez-Palacios & Bautista-Bautista 3491* (MO); Dist. Rivas Dávila, 22-27 km S of Tovar along road to Canaguá, 8°14’ N, 71°45’ W, 2100-2256 m, 16 Apr 1984 (fr), *Luteyn & Luteyn 9977* (MO); Ca 14 km (27 km by road) SE of Azulita on road to Mérida, 2100 m, 3 May 1971 (fl), *Nee & Mori 4140* (MO); same loc., 3 May 1971 (fr), *Nee & Mori 4141* (MO, US); Along quebrada of Cuesta del Barro and Mesa del Trapiche, tributary to Río Capuri, between Canaguá and El Molino, 2530-2715 m, 11 May 1944 (fl), *Steyermark 56486* (F); Los Quebraditos, above Jají, 2590 m, 21 Apr 1944 (fl), *Steyermark 55991* (F); Vertientes del Río Capaz, arriba de La Azulita, 2100-2400 m, 1 Sep 1966 (fl), *Steyermark & Rabe 97105* (US). **Miranda:** Guatopo, 400-600 m, 28 Nov 1956 (fr) *Bernardi 5932* (G); Dist. Paéz, Fila La Tigra, Qda. San Juan, 18 kms al SO de Cúpira, 10°04-05’ N, 65°45-47’ W, 600 m, 2-7 Sep 1977 (fl, fr), *González & Ortega 1170* (MO); Parque Nacional Guatopo, S end of La Macanilla trail, 32 km (by air) NW of Altagracia de Orituco, ca. 10°07’ N, 66°31’ W, ca. 600 m, 27 Aug 1979 (fl, fr), *Nee 17850* (MO); Along Hwy. 12 in Parque Nacional

Guatopo, 9 km S. of junction with Hwy. 1, 25 Apr 1971 (fl), *Nee & Mori 4061* (US); Parque Nacional de Guatopo, bordering Río Santa Cruz, between Santa Teresa and Altagracia de Orituco, 14.5 kms from Los Alpes, 12 kms from Ranchería Mi Querencia, 520 m, 23 Nov 1961 (fr), *Steyermark 89970* (US). **Portuguesa:** 15 kms al este de Chabasquén, 67 kms al NNO de Guanare, 9°26-27' N, 69°54-55' W,1450-1520 m, 29-31 Oct 1982 (fl), *Steyermark et al. 126653* (MO). **Sucre:** Peninsula de Paria, Cerro de Humo, hacia La Roma y Irapa, entre la cumber y La Laguna, noroeste de Irapa, 1060-1273 m, 3 Mar 1966 (fl, fr), *Steyermark 94973* (US). **Tachira:** vicinity of Betania at base of Volcan Tamá, 7°28' N, 72°27' W, 2300 m, 22 Mar 1985 (fr), *Croat 60674* (MO); Alto de Lirio, between Bramón and Las Delicias, 1890-2285 m, 18 Jul 1944 (fl, fr), *Steyermark 57453* (F); along Quebrada Agua Azul, south of El Reposo, 14 km SE of Delicias, 7°31' N, 72°24' W, 2150-2300 m, 22-23 Jul 1979 (fl, fr), *Steyermark & Liesner 118257* (MO). **Trujillo:** Dist. Boconó, Parque Nacional Guaramacal, 9°12'28" N, 70°09'41" W, 1950 m, 19-22 Dec 1995 (fr), *Cuello et al. 1300* (K, MO); Mun. Boconó, Parque Nacional Guaramacal, road from Boconó to Guaramacal, SE of Boconó, 9°13' N, 70°12' W, 2000 m, 13 Jul 1995 (fr), *Dorr & Barnett 8058* (MO); Mun. Boconó, P.N. Guaramacal, between Cerro El Diablo and Qda. Honda, ca. 11 km S of Boconó on road from Fundación La Salle to El Santuario, 9°09' N, 70°17' W, 2100 m, 21 Jul 1995 (fl), *Dorr et al. 8224* (MO); Dist. Boconó, Parque Nacional Guaramacal, trail from la Laguna de las Aguas Negras to la Qda. Salvaje, 9°19' N, 70°11' W, 27 Oct 1998 (fl), *Dorr et al. 8283* (BM, F); Mun. Boconó, Parque Nacional Guaramacal, near Quebrada Honda, 1900-2000 m, 28-29 Dec 2000 (fr), *Dorr & Stergios 8739* (F, MO). **Yaracuy:** Cumbre Gamelatal, 4.3-11 km N of Salom on road from Salom to Candelaria, 10°15' N, 68°29'30" W, 1000-1200 m (fr), *Mori et al. 14656* (F); El Amparo hacia Candelaria, a 7-

10 km al Norte de Salom, 1100-1300 m, 27-30 Dec 1972 (fl, fr), *Steyermark & Espinoza 106813* (MO, US). **No Dept:** Venezuela (fl), *Williams 10486* (F)

Solanum aturense (4) Dunal, Solan. Syn. 32. 1816. — TYPE: VENEZUELA. Orinoco River, Atures, 1800. *A. Humboldt & A. Bonpland s.n.* (Holotype P-HBK!; isotype P photos of holotype (F neg. 38991: F! and Morton neg. 22339: F!), photo of isotype (Morton neg. 8150: F!)

Solanum mirabile Standl. & C.V. Morton, Publ. Field Mus. Nat. Hist. Bot. Ser. 18: 1086. 1938. — TYPE: COSTA RICA. Cartago, San José, Danos los déboisemento a Las Vueltas, Tucurrique, 635 m, Jan 1899, *A. Tonduz 13049* (Holotype US! [1324808]; isotype BM! [BM000579096], G! [G00227713], K! [K000532175], K! [K000532176], M!, W! [W12660])

Solanum siparunoides Ewan, Chicago Acad. Sci., Nat Hist. Misc. 94: 1. 1952. — TYPE: COLOMBIA. Dept. Antioquia, Alto Capiro, above the Sonsón-Abejorral road, 2700-2850 m, 26-28 May 1944, *J.A. Ewan 15766* (Holotype NA (written as USNA in description); isotypes BM! [BM000603441], COL, NO, US! [US2612001])

Names associated with this species that have not been validly published: *Solanum manaense* Sagot ex Lemée, Fl. Guyane Franç. 3: 405. 1954.

Woody vine 1-4 m. Stems moderately to densely armed with recurved, tan to orange roselike prickles, these 2-5 mm long, the base 1-6 x 0.5-1.5 mm, moderately to densely pubescent with tan to rusty, porrect-stellate hairs, the stalks nearly absent to 5 mm, multiseriate, the rays 5-8, 0.5-1 mm, unicellular to multicellular, the midpoints nearly absent. Flowering portions of the stem consisting of difoliate sympodial units, the leaves usually geminate, those of a pair often slightly unequal in size. Leaves simple, the blades 4-16 x 3-9 cm, ovate, leaves chartaceous to coriaceous, slightly discolorous, dark

green adaxially, green to whitish green abaxially, the surfaces sparsely to moderately pubescent with stellate hairs like those of the stem but with the stalks to 1 mm and the midpoints to 1 mm; major veins 4-8 on either side of the midvein, the secondary veins obscure, the midrib abaxially with few to many recurved prickles like those of the stem; base acute, often asymmetrical; margin entire; apex acute; petioles nearly absent to 2.5 cm, moderately pubescent with hairs like those of the stem. Inflorescence 2-10 cm, extra-axillary, unbranched, with 8-20 flowers, the plants andromonoecious, with male flowers on young plants and hermaphroditic flowers on older plants, the axes moderately to densely pubescent with hairs like those of the stem, unarmed; peduncle 1-3 cm; rachis 1-9 cm; pedicels 5-15 mm in flower, 10-20 mm in fruit, filiform in flower, expanding greatly in fruit to 3-5 mm thick, spaced 1-3 mm apart. Calyx 2-5 mm long, the tube 1-3 mm, the lobes 1-2.5 x 1-2 mm, triangular with acute apices, moderately pubescent with hairs like those of the stem, with prickles 1-2 mm, straight to recurved; fruiting calyx 6-10 mm, not accrescent in fruit. Corolla 3-4 cm in diameter, chartaceous, white with occasional purple lines, stellate, lobed nearly to the base, the lobes 12-16 x 1.5-3 mm, narrowly triangular, slightly reflexed at anthesis, acute at the apices, moderately pubescent abaxially with stellate hairs like those of the stem, adaxial surface nearly glabrous. Stamens 12-15 mm; filaments 1-2 mm long, glabrous; anthers 10-14 x 1-2 mm, attenuate, tapering, connivent in bud, connivent to weakly spreading in flower, yellow, the base cordate, the apex obtuse, the pores apical, directed slightly introrsely. Ovary glabrous with occasional glandular hairs; style in functionally male flowers 5-8 x 0.5-1 mm, style in hermaphroditic flowers 13-18 x 0.5-1 mm, exserted beyond the stamens, cylindrical, white, glabrous; stigma to 1.5 mm wide, cylindrical, green. Fruit a leathery berry 1.5-3.5 cm in diameter, globose, greem when immature, orange to red when

mature, glabrous. Seeds 50-100 per fruit, reniform, brown, 3-3.5 x 2-2.5 mm, flattened, the surface netlike with many pits separated by small raised ridges (Fig. 4.11).

Habitat and distribution. (Fig. 4.10) Disturbed roadsides, forest edges, and forest gaps from Veracruz, Mexico through Central America to eastern Colombia and Ecuador at 100-2500 m. *S. aturense* is not found in the Caribbean.

Etymology. The etymology of the *S. aturense* has been difficult to assess. The most obvious implication would be a reference to Atures, Venezuela, especially since the label also indicates the Orinoco River; however, the species is not known from this area. Another possibility is that Pasto in Dept. Nariño, Colombia, was previously referred to as "Atures." (M. Nee pers. comm.). Although Nariño is at the southern edge of the species range, this is a more plausible explaination from a biogeographical standpoint.

Notes. *Solanum aturense* has one of the most extensive ranges of the section and has a correspondingly large variation in phenotypes. Perhaps most conspicuous is the variability in pubescence. Species range from nearly glabrous to densely pubescent with long bristle-like hairs that may reach 5 mm in length. This variability is almost certainly due to environmental conditions and the age of the stem when collected; however, it has caused much confusion and is likely the cause for description of new species (such as the densely pubescent *S. mirabile*) that are at the extremes of the range of variability.

The characteristics that define *S. aturense* are the subcoriaceous leaves that are never lobed and often have a revolute margin. Additionally, the fruits and seeds are the largest in the section and are excellent diagnostic characteristics. The geographical distribution of *S. aturense* is similar to that of *S. volubile* and these species share many morphological similarities. The former species typically has more robust flowers and fruits than *S. volubile*. *Solanum volubile* also has stellate pubescence on the ovary and

base of the style that is absent in *S. aturense*. When flowers and fruits are absent the best character to differentiate these species are the leaves, which are more coriaceous in *S. aturense* and never lobed, whereas those of *S. volubile* are often deeply lobed. Given their similar morphologies, it is unsurprising that *S. volubile* is strongly supported (100% BS, 1.0 PP) as sister to *S. aturense* in phylogenetic results (Stern and Bohs in prep).

The description of *S. aturense* cites a specimen at P-HBK as the type, making this the holotype. The isotype is also at P but is in the general herbarium, not in P-HBK. The name *S. manaense* was published without a Latin description and is therefore invalid under Article 36.1 of the ICBN (McNeill et al. 2006).

Additional specimens examined. BELIZE**. Belize:** Along the Belize River at Burrell Boom, 17°35'N, 88°25'W, 2-5 m, 3 Jan 1995 (fl, fr), *Worthington 23969* (MO).

COLOMBIA**. Antioquia:** cerca de Santa Elena, camino entre Medellín y Rio Negro, ca. 2500 m, 29 Oct 1946 (fl), *Alfaro 22* (US); Santa Elena, 1500-2000 m, 28 Dec 1930 (fr), *Archer 1208* (US); El Páramo de Sonsón, ca. 2600 m, 22 Jun 1948 (fr), *Barkley & Araque 9* (US); 1 km from Termales de Santo Domingo, 5200 ft, 30 Jul 1968 (fr), *Barkley & Barkley 38C529* (US); los alrededores de Angelópolis, ca. 1950 m, 22 Nov 1947 (fl, fr), *Barkley & Gutiérrez 1688* (US); Jarumal, Aug 1943 (fr), *Bro. Daniel 2957* (US); Páramo de Sonsón, 2700-2850 m, 26 Jan 1945 (fr), *Bro. Daniel 3465* (US); same loc., 2 Jan 1947 (fr), *Bro. Daniel 3933* (F, US); Mun. Campamento, vereda El Mango, 6 km al NO de Campamento en la vía a la mina Las Brisas, 7°00'N, 75°21' W, 1820 m, *Callejas et al. 8319* (US); vicinity of Medellín, 1911 (fl), *Charetier 68* (US); Cerca de Santa Elena, ca. 2400 m, 4 Oct 1946 (fl), *Diaz 37* (US); carretera entre Yarumal y Valdivia, region de Ventanas, (fl), *Gutiérrez et al. 6* (US); El Retiro, alrededores de Medellín, 1560 m, 7 Oct 1946 (fl), *Jaimes 40* (US); Piedras Blancas area, above

Medellín, 1 km from Escuela de Peritos Forestales, 6°16'N, 75°31' W, 2200-2600 m, 1 Apr 1981 (fl), *Nee & Mori 3889* (US); cerca de Santa Elena, camino entre Medellín y Río Negro, ca. 2300-2500 m, 1946 (fl), *Pérez 292* (US); Urrao Municipio, Las Orquídeas, Vereda Calles, Parque Nacional Natural Las Orquídeas, Quebrada Honda, Inventario Permanente de bosque húmedo premontano, en el filo al NW de La Cabaña Calles, parcela W, subparcelas W8-W9, W-10, 6°29'N, 76°14'W, 1300 m, 11 Dec 1992 (fr) *Pipoly et al. 17059* (GH, K); Medellín, camino de Mazo, cerca a la Laguna de Guarne, 2600 m, 27 Jul 1951 (fl), *Uribe 2182* (US); La Sierra de la carretera a Guarne, ca. 2500 m, 19 May 1948 (fr), *Valderrama 275* (US). **Boyacá:** Vicinity of Boavita, 2250 m, 16 Sep 1938 (fl), *Cuatrecasas 1918* (F); carretera de Chiquinquira a Saboyá, 2600 m, 2-3 Dec 1958 (fr), *García-Barriga 16235* (US); Río Pomera, 12 km NW of Aracbuco, 1755 m, 20 Aug 1944 (fr), *St. John 20678* (US). **Caldas:** a unos 20 kms de Puente de Linda hacia La Dorada, (fl), *Gutiérrez et al. 2-G* (US). **Caquetá:** Comisaría del Caquetá, Cordillera Oriental, vertiente oriental, Sucre, 1000-1300 m, 4 Apr 1940 (fl), *Cuatrecasas 9063* (F, US). **Cauca:** carretera entre Popayán y San Joaquín, cerca al Río Los Robles, 1700-1800 m, 30 Sep 1954 (fl), *Fernández 2708* (US). **Chocó:** Mun. de Riosucio, Zona de Urabá, Región del Cerro del Cuchillo, 100-400 m, 19 Jan 1988 (fr) *Cárdenas 1092* (MO); Hydro Camp 6, Alto Truando, ca. 2500 ft, 8 Mar 1968 (fl), *Duke 15344* (US); Mun. de San José del Palmar, hoya del Rio Torito (afluente del Rio Hábita), 850-950 m, 16 Mar 1980 (fr), *Forero et al. 7378* (US); Area of Baudó, on the right side of Rio Baudo, about 1 km upstream from the village of Point Pizarro, 11 Feb- 29 Mar 1967 (fr) *Fuchs & Zanella 22174* (K, US); carreterra de Quibdó a Yuto, a unos 10 kms. de Quibdó, ca. 350 m, 21-24 Jun 1962 (fl), *Gutiérrez 2893* (GH, US); Bahia Utria, along Río Sampechi, sea level, 1 Feb 1947 (fl), *Haught 5513* (US); Istmina, on Río San Juan, ca. 75

m, 29 Apr 1939 (fl), *Killip 35478* (US); Rio Taparal off Rio San Juan, 100 ft, 29 Aug 1962 (fl), *Robinson 366* (US). **Cundinamarca:** Hacienda La Carlina, San Francisco, ca. 7500 ft, 20 Aug 1939 (fl), *Balls 7427* (BM, US); Mun. de La Mesa, "Potrero del Rodeo", al noroeste de La Mesa, 1200-1300 m, 17 May 1952 (fl), *Fernández & Mora 1398* (US); al oeste de Guaduas, camino de herradura entre Guaduas y el Alto de Aguaclara, hacienda "Paramillo", 1040-1320 m, 24 Jul 1947 (fl), *García-Barriga 12354* (US); Santandercito, abajo del Salto de Tequendama, 1540 m, 4 Mar 1976 (st), *García-Barriga 20953* (US); San Francisco Road, 30 Aug 1947 (fl), *Haught 6121* (US); Pacho, 1600-2200 m, Jan (fl), *Lehmann 7567* (K, F); About 5 km from Fusa on road to Arbelaez, Jun 1967 (fl), *Martin & Plowman 112* (GH, K, US); Fusagasuga to Pandi, 1000-1300 m, 30 Nov 1917 (fl), *Pennell 2747* (GH); Mun. de Silvania, Vereda San Luis Bajo, ca. 1800 m, 22 Mar 1988 (fl), *Sanabria et al. 220* (US); Viotá, vereda de Liberia, 1450 m, 30 Dec 1967 (fl), *Uribe 6028* (US). **Magdalena:** San Sebastián de Rábago, 13 Mar 1948 (fl), *Castañeda 942* (US); San Sebastian, Sierra Nevada de Santa Marta, 6200 ft, 17 Aug 1946 (fl), *Foster & Smith 1519* (GH); Santa Marta, 4500 ft, 1898-1901 (fl), *Smith 1155* (BM, BR, F, G, GH US). **Meta:** Los Llanos, Int. El Meta, Villavicencio, 11 Nov 1938 (fl), *Cuatrecasas 4714* (US); Cumaral (fr), *Ed. André K653* (K); Via Villavicencio (fl), *Ed. André K654* (K); Uribe, Int. de Meta, 770 m, 19 Dec 1942 (fl), *Fosberg 19428* (US); Along Río Guatiquía, near Villavicencio, ca. 500 m, 18-19 Mar 1939 (fr), *Killip 34425* (US); Sierra de la Macarena, Río Guapaya, 450 m, 29 Nov 1949 (fl), *Philipson et al. 1625* (BM, US); same loc., 30 Nov 1949 (fl, fr), *Philipson et al. 1653* (BM, GH, US); Villavicencio, road to Restrepo, about 5 mi from Villavicencio, 23 Jul 1945 (fl, fr), *Schiefer 835* (GH, MO, US). **Quindio:** Quindio? (fr), *Ed. André K652* (K); San Juan, 8 Mar 1876 (fr), *Ed. André 2046* (K); same loc., (fl), *Ed. André 2148* (K); Mun. de

Filandia, Vereda La Julia, carretera Filandia-La India, Finca Campoalegre, 1600 m, 3 Feb 1995 (fr), *Vélez et al. 4907* (M). **Tolima:** Dolores, 1600-2000 m, Apr (fl), *Lehmann 7327* (F, K); Toche, 2500 m, 25 Oct 1942 (fr), *Sneidern 3127* (GH). **Valle:** Cordillera Occidental, vertiente occidental, hoya del Río Anchicayá, lado izquierdo, El Prado, 250-350 m, 4 Aug 1943 (fl, fr), *Cuatrecasas 14859* (F, US); Río Calima (Región del Chocó), La Trojita, 5-50 m, 23 Feb 1944 (fl, fr), *Cuatrecasas 16376* (F, US); Costa del Pacífico, Río Cajambre, Barco, 5-80 m, 21-30 Apr 1944 (fr), *Cuatrecasas 17152* (F, US); Mun. Buenaventura, Corr: Chanco, orilla Río Calima, 450 m, 17 Feb 1989 (fr), *Devia & Prado 2497* (US); Mun. Restrepo, Río Calima, Cusumbo, 680 m, 21 Feb 1989 (fl), *Devia & Prado 2585* (US); Colorado, north shore of Buenaventura Bay, 5-15 m, 3 Jun 1944 (fr), *Killip & Cuatrecasas 38714* (US); Carretera from Buga to Darien, bosque de los Muertos, 1200 m, 19 May 1982 (fl), *Murphy 417* (US); Darien, along carretera Campo Alegre, 1600 m, 21 May 1982 (fl, fr), *Murphy 456* (US). **Valle del Cauca:** Mun. Buenaventura, community of San Isidro, 3°59’ N, 76°57’ W, 230 m, 15 Nov – 6 Dec 1979 (fr), *von Rooden et al. 355* (K); **No dept:** Prov. de Bogota, Ubalá, 1900 m, 1851-1857 (fl), *Triana 2231* (W).

COSTA RICA**. Alajuela:** UCR Reserva, Fila Volcan Muerte, between the headwaters of the Rio San Lorenzo and Bajo Jamaical, 1000-2000 m, 15-17 Apr 1982 (fl), *Barringer & Gomez-Laurito 2591* (F); Cantón de San Ramon, Bosque Eterno De Los Niños, Codillera de Tilarán, Valle del Río Peñas Blancas, 10°20’21”N, 84°40’38”W, 900-1000 m, 7 Oct 1993 (fr), *Bello & Cruz 5362* (BM); Baja La Palma de San Ramon, 17 Apr 1927 (fl), *Brenes 5425* (F); Entre Rio Jesús y Calera de San Ramón, 16 Feb 1933 (fl), *Brenes 17061* (F); About 3 km NNE of Bijagua along the new road to Upala, 10°45’N, 85°03’W, 450 m, 7-8 Nov 1975 (fl), *Burger & Baker 10021* (F); Caribbean

slopes near the falls of the Rio La Paz and along the road to Puerto Viejo, 10°12'N, 84°10'W, 1400-1500 m, 19-21 Feb 1982 (fl), *Burger et al. 11869* (F);); Cerro de Santiago, San Ramón, 1100 m, 29 Apr 1982 (fr) *Carvajal 231* (MO); Karibische Seite der Cordillera de Tilarán, weg zur station am Río San Lorencito in der Reserva Forestal de San Ramón zwischen dem Abzweig zur Colonia Palmareña (500 m nördlich der Brücke über den Río San Lorenzo) und dem Beginn des Schutzgebietes (ca. 20 km Luftlinie NW von San Ramón), 750-800 m, 22 Mar 1991 (fl,fr) *Döbbeler 5075* (M); Cordillera de Tilarán, nordwestliche Umgebung von San Ramón, Reserva Biológica Albreto Brenes, zugangsweg zur Station am Río San Lorencito (etwa 20 km Luftlinie NW von San Ramón, 850-900 m, 12 Oct 1995 (fl), *Döbbeler 6034* (M); Volcan Poas, 2000 m, Mar 1896 (fl), *Donnell Smith 6664* (K, K); Cantón de Upala, P.N. Guanacaste, Estación San Ramón, Dos Ríos, Sendero el Níspero, 10° 52'50"N, 85°24'05"W, 550 m, 16 Mar 1993 (fr), *Espinoza 811* (BM); Upper drainage of the Río Peñas Blancas below the Monteverde Cloud Forest Nature Reserve, 9°17'N, 84°86'W, 1250-1350 m, 25-26 Feb 1977 (fl, fr), *Gentry 3803* (F); Reserva Forestal de San Ramón, 10°13'N, 84°37'W, 900-1200 m, 16-19 Apr 1987 (fl, fr), *Gomez-Laurito 11478* (F); San Carlos, margen del Río Peñas Blancas, a la altura de San Pedro, 29 Jun 1985 (fr), *Haber & Bello 1760* (MO); Near Rio Penas Blancas. Caribbean side of the Continental Divide, ca 1400 m, Aug 1981 (fr), *Hepper 75* (BM); 6.5 km S of Ciudad Quesada, 1120 m, 10 Sep 1967 (fl), *Lent 1270* (F, GH); 10 km NNW of San Ramón by road on way to San Lorenzo, 2.5 km S of Balsa, 10°09'N, 84°29'W, 1200 m, 25 Apr 1983 (fl, fr), *Liesner & Judziewicz 14972* (MO); 15 km NW of San Ramón by air, cerro Azahar, headwaters of Río San Pedro, 10°09'30"N, 84°34-35'W, 1400-1500 m, 14 May 1983 (fr), *Liesner et al 15540* (MO); Cantón de Upala, P.N. Guanacaste, Cordillera de Guanacaste, Estación San Ramón, Dos Ríos,

Sendero La Argentina 10°52’50”N, 85°24’05”W, 550 m, 24 Jan 1995 (fr), *Quesada 165* (BM); Region of Zarcero (fl), *Smith 344* (F); San Luis de Zarcero, canton Alfaro Ruiz, 1450 m, 18 May 1938 (fl), *Smith 627* (F); Alajuela and Puntarenas border, in “Los Cerros Centinales” near Quaker settlement at Monteverde, 1500 m, 5 May 1975 (fl), *Utley & Utley 2425* (F Cordillera Central near San Juan de Laja about 15 km north of Zarcero, 1350 m, 7 Feb 1965 (fl, fr), *Williams et al. 29035* (F). **Cartago:** Hills above El Muneco, along Rio Sombrero, 9°45’N, 83°55’W, 1500 m, 28 Jul 1983 (fl), *Barringer & Christenson 4126* (F); Hillside overlooking Rio Grande de Orosi, about 3 km SE of Tapantí, 1400 m, 16 Apr 1967 (fl), *Lent 818* (F, GH); Above Río Taus, Selva, 9°47’N, 83°45’W, 950 m, 2 Aug 1972 (fr), *Lent 2754* (MO); Quebrada Quebradas, 9 km SE of San José, 1450 m, 9°53’N, 84°01’W, 19 Dec 1976 (fr), *Lent 4001* (F); 1300 m, Jul 1888 (fl,fr) *Pittier 555* (BR). **Guanacaste:** Zona Protectora Tenorio Tierras Morenas, Tilarán, Río San Lorenzo, 10°36’30”N, 85°00’00”W, 1050 m, 24 Mar 1991 (fl), *Alvarado 114* (K); Santa Cruz, Cordillera de Guanacaste, Finca La Pasmompa, 5 km al Sur de Santa Cecilia, 11°02’00”N, 85°24’30”W, 450 m, 7 Sep 1992 (fr) *Espinoza 549* (BM); Eastern slopes of Volcán Miravalles (Cerro la Giganta) above the town of Río Naranjo near the Continental Divide, 10°42’N, 85°7’W, ca. 800 m, 8 Apr 1973 (fl, fr), *Gentry & Burger 2895* (MO); Santa Elena to Tilarán road, Florida, c. 1100 m, 17 Feb 1984 (fr), *Khan et al. 1129* (BM); Vicinity of Santa Elena, 1600 m, 28 Apr 1980 (fl), *Meerow et al. 1042* (F); Z.P. Tenorio, Tilarán, Cord. V. Tilarán, Tierras Morenas, Río San Lorenzo, 10°36’40”N, 84°59’45”W, 1000 m, 23 Mar 1993 (fl), *Rodríguez & Jiménez 79* (BM, MO). **Heredia:** Finca La Selva, Puerto Viejo, 90 m, 13 Oct 1968 (fl), *Frankie 10a* (F, MO); Gorge of the Río Peje, Atlantic slope of Volcán Barva, 10°19’N, 84°04.5’W, 480-500 m, 6 Apr 1986 (fl), *Grayum 6813* (MO); Finca La Selva, the OTS field station on the Río Puerto Viejo

just E of its junction with the Río Sarapiquí, south boundary line, new property, 3991NS x 1200 EW m line, 22 Sep 1982 (fl, fr), *McDowell & Santana 183* (MO); Au fried du Carrizal, mas sef du Barva, 1600 m, Jan 1889 (fl), *Pittier 804* (BR, G); Barva, no protegida, Cuenca del Tárcoles, San José de la Montaña, ca. 2 km del Cruce de Porrosatí, ruta al Volcán Barva, 10º06'43"N, 84º07'17"W, 2260 m, 9 Feb 2000 (fl, fr), *Rodriguez et al. 5708* (G); South slopes of Volcan Barba between Rio Ciruelas and Sacramento, 2100 m, 3 May 1975 (fr), *Utley & Utley 2325* (F). **Limón:** Talamanca, R.V.S. Gandoca-Manzanillo, Puerto Viejo, en sendero, a orilla de la costa de Manzanillo hacia Gandoca, 9º38'00"N, 82º38'26"W, 10 m, 4 Oct 2000 (fr), *Acosta et al 2852* (G); Cantón de Pococi, R.N.F.S., Barra del Colorado, Llanura de Tortuguero, Sardinas, 10°38'38"N, 83°44'10"W, 15 m, 25 Nov 1992 (fl), *Araya 123* (BM); Ca. 4-5 airline km S of Islas Buena Vista, in the Rio Colorado, 10°38'40"N, 83°41'00"W, 100-180 m, 17 Sep 1986 (fr), *Davidse & Herrera 31306* (F, MO); Jiménez, Llanos de Santa Clara, Comarca de Limón, 650 ft, Apr 1894 (fr), *Donnell Smith 4896* (GH, K); Jiménez, Llanuras de Santa Clara, 250 m, Feb 1896 (fl, fr), *Donnell Smith 6666* (BM, GH); Chirripó National Park, path from Agua Potable to lowest edge of forest, near San Gerardo, 1300-2000 m, 19 Feb 1983 (fl), *Garwood et al. 1389* (BM); Along hwy C.R. 233, 8 km north of Tres Equis, 400 m, 24 Apr 1965 (fl, fr), *Lent 534* (F, MO); Cantón de Limón, Cerro Muchilla, Fila Matama, Entrando por pueblo El Progreso, 9°47'40"N, 83°06'30"W, 750 m, 13 Apr 1989 (fr), *Robles & Chacón 2776* (BM); Cerro Coronel, E of Río Zapote, along and above near road, 10°40'N, 83°40'W, 10-100 m, 24 Jan 1986 (fl, fr), *Stevens 23952* (F, MO). **Puntarenas:** Area between the Rio Esquinas and Palmar, 100 fr, 8 Apr 1949 (fl, fr), *Allen 5236* (F); Between Agua Buena and the escarpment above Villa Neil, about 8°44'N, 82°56'W, 1000 m, 19 Jan 1967 (fl), *Burger & Matta 4587* (F, US); Foothills of

the Cordillera de Talamanca, directly N of Las Alturas, ca. 8°57'N, 82°50'W, 1400-1500 m, 28 Aug 1983 (fl, fr), *Davidse 24167* (MO); Parque Internac. La Amistad, San Vito, Coro Brus., Finca Cafrosa, 8°54'15"N, 82°46'50"W, 500 m, 4 Jul 1990 (fr), *Delgado 37* (F); Ca. 2 km southeast of Monteverde, 10°18'N, 84°48'W, 1500-1550 m, 18-21 Mar 1973 (fl), *Gentry & Burger 2682* (MO); East of Quepos, Pacific slope of the Talamanca Range, 9°29'N, 84°03'W, 350-450 m, 19 Feb 1977 (fl), *Gentry 3766* (F); East of Quepos, Pacific slope of the Talamanca Range, 9°29'N, 84°03'W, 150-250 m, 19 Feb 1977 (fr), *Gentry 3769* (F); Monteverde, 10°47'N, 84°50'W, 1450-1550 m, 21 Aug 1984 (fr), *Gentry & Haber 48739* (MO); San Vito de Java, finca "Las Cruces", Feb 1971 (fr), *Gillis & Plowman 10110* (F); Rincón, Peninsula de Osa, 150 m, 4 Mar 1965 (st) *Jiménez 3036* (F, GH, US); Jamaical, Montes de Oro, 1000 m, May 1961 (fl), *Jiménez s.n.* (F); Parque Nacional Corcovado, Lower Lookout Trail, 8°27-30'N, 83°33-38'W, 50-100 m, 1 Aug 1988 (fl), *Kernan & Philips 751* (MO); Parque Nacional Corcovado Sirena, Río Claro, 8°28'N, 83°35'W, 1-20 m, 25 Aug 1989 (fl), *Kernan 1235* (MO); Parque Nacional Corcovado, ridges above Río Claro, 8°28'N, 83°35'W, 0-100 m, 24 Nov 1981 (fr), *Knapp & Mallet s.n.* (MO); Osa Peninsula, Corcovado National Park, along trail and in forest between headquarters to Sirena and Pavo, 8°30'N, 83°36'W, 0-10 m, 5 Jul 1977 (fl, fr), *Liesner 2876* (MO); Res. Forestal Golfo Dulce Bahía de Chal, ca. 5 km al N de Rincón, 8°44'N, 83°27'W, 50-150 m, 20 Aug 1990 (fl), *Morales & Chacón 80* (MO); Cantón de Golfito, R.N.V.S. Golfito, Valle de Coto Colorado, Golfito, camino en la Fila Gambas, sector oeste, 8°40'19"N, 83°12'52"W, 325 m, 10 Aug 1994 (fl), *Morales 3093* (MO); Río Agua Buena, 1 km downstream from OTS camp, 5 km W of Rincón, 40 m, 7 Mar 1971 (fr), *Nee & Mori 3556* (US); Monteverde, Cloud Forest Reserve, Cordillera de Tilarán, pacific slope of Continental Divide, 1500-1620 m, 1 Sep 1984 (fr), *Pounds 313*

(MO); Camino de Altura, 6 mi west of Rincón de Osa, about 1000 ft, 21 Mar 1967 (fl), *Raven 20840* (F); Camino de Altura, 2 to 5 miles west of Rincon de Osa, Osa Peninsula, 400-1000 ft., 3 Aug 1967 (fl), *Raven 21509* (MO); Osa Peninsula, along the Camino de Altura, 2 to 5 miles west of Rincon de Osa, trail to airfield from mile 4, about 500 ft., 9 Aug 1967 (fr) *Raven 21675* (F); Above Wilson's Finca, 6 km south of San Vito de Java, about 5000 ft, 17 Aug 1967 (fl), *Raven 21878* (F); Wilson's finca, 6 km south of San Vito de Java, about 4000 ft, 19 Aug 1967 (fl, fr), *Raven 21976* (F); Río Corozal, Comarca de Puntarenas, Apr 1896 (fl, fr), *Tonduz 7091* (K- 2 sheets, US); Finca of Compania Las Alturas, 10-15 km east by ENE of the town of La Union near the Costa Rican Panamanian border or about 30 km NE of San Vito de Java, 12 May 1976 (fl), *Utley & Utley 4811* (F, MO); Monteverde, ca. 1700 m, 17-18 Apr 1967 (fl), *Weston & Weston 4782* (F). **San José:** La Palma area, northeast of San Jeronimo, above La Hondura valley, 10°02'N, 84°0'W, 1500 m, 15 Sep 1978 (fl, fr), *Burger & Antonio 11075* (F); Z.P. Cerros de Escazú, 9°49'39"N, 84°06'05'W, 1700-1800 m, 15 Jul 1991 (fl, fr), *Morales 34* (BM); Vicinity of El General, 1010 m, Feb 1936 (fl), *Skutch 2588* (GH); Vicinity of El General, 1000 m, Feb 1939 (fl), *Skutch 4218* (K); San Marcos, Tarrazú, Fila San Isidro, 9°34'20"N, 84°04'10"W, 1300-1400 m, 5 Nov 1997 (fr), *Valverde et al. 379* (F); Cordillera de Talamanca, about 25 km north of San Isidro de El General along Pan American Highway, 3200 m, 29 Jan 1965 (fr), *Williams et al. 28631* (F). **No Province:** Carretera a Guápiles, 1500 m, 21 Jan 1988 (fl), *Pineda 256* (K); Marais a La Palma, v. Pacif., 1550 m, 18 Dec 1888 (fl), *Pittier 686* (BR); Vara Blanca de Sarapiquí, north slope of Central Cordillera, between Poás and Barba volcanoes, 1680 m, Oct 1937 (fl), *Skutch 3343* (A, K)

ECUADOR. **Bolivar:** Limon, estrivaciones inferiors de la cordillera occidental, 800 m, 19 Oct 1943 (fr) *Solís 6434* (F). **Carchi:** Maldonado, Parroquia Tobar Donoso, reserva etnica Awá, 00°55’ N, 78°32’ W, 900 m, 22 Nov 1992 (fl), *Aulestia et al. 799* (MO); above San Marcos de los Coaiqueres on trail towards Gualpí Bajo, 1000 m, 7 Feb 1985 (fr), *Øllgaard 57496* (BM); Tulcan Canton, Parroquia Tobar Donoso, Reserva Indígena Awá, 01°00’ N, 78°24’ W, 650-1000 m, 19=28 Jun 1992 (fl), *Tipaz et al. 1248* (BM). **Cotopaxi:** Mun. Cantón La Maná, Reserva Ecológica Los Ilinizas, Cerro Tilipulo, filo de cumber, Cordillera Tilinche, 0°46’30”S, 79°05’45”W, 2022 m, 25 Jul 2003 (fr), *Silverstone-Sopkin et al. 9524* (MO). **Esmeraldas:** Mun. de Lita, road from Lita to San Lorenzo, 19 km N of Lita, ca. 650 m, 10 May 1987 (fl), *Acevedo & Daly 1661* (F, US); San Lorenzo Canton, Reserva Etnica Awá, centro Guadualito, 01°15’N, 78°40’W, 20-29 Jul 1992 (fr), *Aulestia et al. 42* (BM); Km 12, Cristal, Lita-(La Merced de) Buenos Aires, edge of Cotacachi Cayapas Reserva Ecologica, 20 Jul 1988 (fr), *Dodson 17578* (BM); NW of Lita, km 18-40, 00°58’N, 78°35’W, 600-900 m, 28 Sep 1991 (fr), *Øllgaard 1317* (MO); Eloy Alfaro, Reserva Ecológica Cotacachi-Cayapas, Charco Vicente, Río San Miguel, afluente del Río Cayapas, 00°43’ N, 78°53’ W, 150 m, 6-9 Sep 1993 (fl), *Palacios & Tirado 11272* (BM); San Lorenzo Canton, Alto Tambo, 15 km W of Lita, 00°50’N, 78°32’W, 400 m, 9 Sep 1990 (fl, fr), *Rubio & Carlos 635* (F); San Lorenzo Canton, Parroquia Ricaurte, comunidad Balsareño a 10 km al este de Ricuarte, reserva AWA, 01° 09’ N, 78°31’ W, 80 m, 15-29 Apr 1991 (fr), *Rubio & Quelal 1448* (BM); Eloy Alfaro, Reserva Ecológica Cotacachi-Cayapas, Charco Vicente, Río San Miguel, 00°43’ N, 78°53’ W, 200 m, 20-31 Sep 1993 (fr), *Tirado et al. 380* (BM); Eloy Alfaro, Reserva Ecológica Cotacachi-Cayapas, Parroquia Luis Vargas Torres, Río Santiago, estero Pote, 00°49’ N, 78°45’ W, 250 m, 23-27 Oct 1993 (fl), *Tirado et al 497* (BM,

MO).**Imabura:** Cotacachi, Parroquia García Moreno, Reserva Biológica Los Cedros, sendero El Observatorio, 00°17’28” N, 78°47’13” W, 1690 m, 28 Oct 2005 (fr), *Vargas et al. 6368* (MO). **Los Rios:** Ridge line at El Centinela at crest of Montanas de Ila on road from Patricia Pilar to 24 de Mayo at km 12, 600 m, 23 May 1983 (fr), *Dodson & Benzing 13908* (F); Quevedo Canton, Parroquia Centinela-La Pirámide, Vía Santo Domingo de los Colorados-Quevedo entrando por Patricia Pilar km 41, 01°40’S, 79°20’W, 650 m, 25 Feb 1992 (fl), *Quelal & Tipaz 275* (BM). **Pichincha:** Carretera Quito-Puerte Quito, km 113m 10 km al norte de la carretera principal, 00°05’ N, 79°02’ W, 800 m, 27-29 Dec 1983 (fl, fr), *Balslev & Balseca 4721* (MO).

GUATEMALA**. Izabal:** Montañas del Mico, 7-8 km W of Santo Tomás de Castilla on road to microwave tower, 600-650 m, 19 Aug 1988 (fr), *Stevens et al 25537* (F, K, MO) **Suchitepéquez:** Southwestern lower slopes of Volcán Zunil, bordering quebradas and barrancos between Finca Montecristo and Finca Asturias, southeast of Santa María de Jesús, 1200-1300 m, 1 Feb 1940 (fr), *Steyermark 35283* (US).

HONDURAS**. Cortes:** Montana de Cusco, Cordillera de Idalfonso, 1500-2000 m, 26 May 1956 (fl), *Molina 7265* (F). **Yoro:** Río Guán Guán, 15°30’00”N, 87°27’20”W, 300-380 m, 24 Apr 1995 (fl, fr), *Hawkins & Merello 817* (MO).

MEXICO**. Veracruz:** Lado W de Cerro Mastagaga, ca. 13 km al NE de San Andres Tuxtla, San Andres Tuxtla, 18°31’N, 95°09’W, 1200 m, 29 Jan 1972 (fr), *Beaman 5559* (F); Cerro Cintepec al E de Zapoapan, Catemaco, 18°19’N, 95°01’W, 900 m, 8 Feb 1972 (fr), *Beaman 5609* (F); Cerca de 10 km al NE de Tapalapan, San Andres Tuxtla, 18°35’N, 95°13’W, 450 m, 31 May 1972 (fr), *Beaman 6026b* (F); Mun. San Andres Tuxtla, Estación Biologica de Los Tuxtlas, 1200 m, 9 Dec 1969 (fr), *Calderón 2124* (F); Mun. México, El Bastonal, 720 m, 27 Jan 1978 (fr), *Calzada 4253* (F); Mun. Soteapan,

Faldas del Cerro Platanillo, Sierra de Santa Martha, 18°26'N, 94°57'W, 1380 m, 20 Dec 1978 (fr), *Calzada 5071* (F); Estacion Biologica de Los Tuxtlas, San Andres Tuxtla, 120 m, 9 Dec 1969 (fr), *Martinez 2124* (MO); Along dirt road 13 km E of Tebanca (13 km E of east side of Lago Catemaco) on way to Santa Marta, Mun. Soteapan, 800-950 m, 5 Jul 1980 (fl), *Nee & Hansen 18812* (F); San Pedro Soteapan, Ejido Santa Martha, 18°25'N, 94°56'W, 1250 m, 11 Nov 1980 (fr), *Vázquez & Hernández 20* (F); Lomas Santa Rita, municipio de Yecuautla, 1400 m 13 Mar 1971 (fl), *Ventura A. 3274* (F); El Cajón, municipio de Yecuatla, 1150 m, 16 Nov 1973 (fr), *Ventura A. 9268* (F). **No Dept:** No loc, 1938 (fl), *Balls s.n.* (K).

NICARAGUA**. Matagalpa:** 16-18 km al NE de la ciudad, sobre la carretera al Tuma, 12°59'N, 85°49'W, 600-700 m, 21 Oct 1981 (fl), *Guzmán & Castro 2046* (MO) **Zelaya:** Ca 6.3 km S of bridge at Colonia Yolaina and ca. 0.8 km of ridge of Serranias de Yolaina on road to Colonia Manantiales (Colonia Somoza), ca. 11°36-37'N, 84°22'W, ca. 200-300 m, 13-14 Feb 1978 (fl), *Stevens 6400* (BM, MO).

PANAMA**. Bocas del Toro:** Changuinola, PILA, 9°03.619'N, 82°42.992'W, 1500 m, 18 Apr 2008 (fl), *Monro et al. 6017* (BM). **Chiriquí:** Vicinity of Fortuna Dam, along roadside on N side of lake, ca 1100 m, 11 Feb 1987 (fl), *Bohs & McPherson 2320* (F); 8 miles west of Puerto Armuelles in vicinity of San Bartolo Limite, 19 Feb 1973 (fl), *Croat 22025* (F); Trail west from Fortuna Dam Camp to La Fortuna, 8°43'N, 82°14'W, 1300 m, 13 Mar 1985 (fl, fr), *Hampshire & Whitefoord 558* (BM). **Coclé:** El Valle, 800-1000 m, 28 Jun 1967 (fr), *Duke 13153* (US). **Panamá:** El Llano-Carti road 10 miles from Interamerican Highway near El Llano, 330 m, 28 Mar 1976 (fl), *Croat 33813* (BM); To Udirbi, around Udirbi, El Llano-Cartí road, 200-350 m, 1 Jul 1984 (fr), *D'Arcy et al. 16034* (BM, G, K); Altos de Pacora, 9°14'N, 79°21'W, 2 Apr 1997 (fr), *Galdames et al.*

3773 (F); Barro Colorado Island, lab clearing, shoreline near base of stairs, 22 May 1986 (fr), *Garwood 1833a* (BM, F); Nusagandi and road to Carti, 9°18'N, 78°58'W, 400 m, 18 Jul 1986 (fr) *McDonagh et al. 130* (BM); Comarca De San Blas, Nusagandi and road to Carti, 9°18'N, 78°58'W, 400 m, 18 Jul 1986 (fr) *McDonagh et al. 160* (BM); Comarca San Blás, Kuna Yala, 6 km before Nusugandé on Llano-Carti road, 9°19'11"N, 78°59'57"W, 370 m, 25 Aug 2000 (fr), *Monro et al. 3539* (BM); Nusagandi, sede de campo de PEMASKY, aprox. 20 km on El Llano-Carti Road, aprox. 9°18'N, 78°59'W, 350 m, 29 Apr 1992 (fr), *Paredes et al. 883* (F); El Llano-Cartí Road, 20 km from Pan Am Hwy, 9°16'N, 78°58'W, 900-1000 ft, 12 Sep 1980 (fl), *Sytsma 1080* (US). **Veraguas:** 7 km W of Santa Fe on new road past agricultural school, ca. 2900 ft., 12 Apr 1974 (fl), *Nee 11201* (GH).

Solanum flexicaule (5) Benth., Bot. Voy. Sulph. 141. 1845. — TYPE: ECUADOR. Guayas: Guayaquil, 1841, *Hinds s.n.* (lectotype, **here designated** K! [K000449564]).

Shrub 1-6 m, scandent on other vegetation. Stems sparsely armed with recurved tan to orange roselike prickles, these 1-3 mm long, the base 0.5-1x 0.2-0.5 mm, moderately pubescent with tan, porrect-stellate hairs, the stalks nearly absent to 1.5 mm, multiseriate, the rays 4-8, 0.5-1 mm, unicellular to multicellular, the midpoints nearly absent. Flowering portions of the stem with difoliate sympodial units, the leaves geminate, those of a pair slightly unequal. Leaves simple, the blades 4-8 (11) x 1-3 cm, ovate, chartaceous, slightly discolorous, dark green adaxially, green abaxially, the adaxial surface moderately pubescent with stellate hairs like those of the stem but the stalks absent and the midpoints to 1 mm, the abaxial surface densely pubescent with stellate hairs like those of the stem; major veins 4-6 on either side of the midvein, the midrib abaxially with a few to many recurved prickles like those of the stem but 0.5-1 mm long;

base acute, occasionally asymmetrical; margin entire or with 2-3 obtuse lobes per side, the sinuses cut less than 1/6 of the way to the midvein; apex acute; petioles 4-10 mm, moderately to densely pubescent with stellate hairs like those of the stem, unarmed or with 1-2 recurved prickles like those of the stem. Inflorescences 3-6 cm, extra-axillary, unbranched, with 4-6 flowers, the plants apparently andromonoecious, the axes moderately to densely pubescent with hairs like those of the stem, unarmed; peduncle nearly absent to 6 mm; rachis 2.5-5.5 cm; pedicels 5-8 mm in flower, 7-10 mm in fruit, filiform, spaced 1-2 mm apart. Calyx 4-6 mm long, the tube 4-5 mm, the lobes 1-2 x 0.2-0.5 mm, narrowly triangular, moderately pubescent with stellate hairs like those of the stem, armed with straight prickles 0.5-1 mm in length; fruiting calyx 6-10 mm, the lobes often reflexed, not accrescent in fruit. Corolla 1.5-2.5 cm in diameter, chartaceous, white to lilac, stellate, lobed nearly to the base, the lobes 7-10 x 1.5-2.5 mm, narrowly triangular, densely pubescent abaxially with hairs like those of the stem, glabrous adaxially except a few stellate hairs along the midvein. Stamens 8-12 mm; filaments 1-1.5 mm long, glabrous; anthers 7-9 x 1-2 mm, attenuate, tapering, connivent, yellow, the base cordate, the apex obtuse, the pores apical, directed slightly introrsely. Ovary densely pubescent with stellate hairs like those of the stem; style in functionally male flowers 3-5 x 0.5-1 mm, style in hermaphroditic flowers 10-14 x 0.5-1 mm, exserted beyond stamens, cylindrical, white, pubescent at proximal end with hairs like those of the ovary, distal end becoming glabrous; stigma 0.5-1 mm wide, green. Fruit a thin-skinned berry, 1-2 cm in diameter, globose, green when immature, orange-red when mature, initially with scattered stellate hairs like those of the ovary, becoming glabrous. Seeds 20-40 per fruit, 2.5-3 x 2-2.5 mm, nearly round, brown, flattened, the surface netlike with many pits separated by small raised ridges (Fig. 4.12).

Habitat and distribution. (Fig. 4.13) Due to the lack of collections, little is known about the habitat of *S. flexicaule*. Presently it is known from only Los Rios, and Guayas provinces in Ecuador at 400-700 m with another probable specimen from Esmeraldas, Ecuador.

Etymology. The epithet is derived from the Latin "flexi-" meaning "bending" and "-caule" meaning "stem" and refers to the pliant stem of the species that is likely necessary for the its climbing, scrambling habit.

Notes. *Solanum flexicaule* is only known from a small area in the lowlands of western Ecuador. This area has been heavily deforested and used for cultivation; this is a likely cause for the few collections of *S. flexicaule* (Dodson and Gentry 1991). Recent collections of *S. flexicaule* have been made near Cerro Samama in Los Rios Prov., Ecuador. A recent trip to Ecuador by the author found much of this area under cultivation and was unsuccessful in locating *S. flexicaule*.

Herbarium specimens of *S. flexicaule* have been annotated as *S. volubile* (or its synonym *S. adhaerens*). These species share many morphological characteristics, but *S. flexicaule* can be differentiated by its densely pubescent unlobed leaves and by its slightly smaller fruits and flowers as well as its disjunct distribution.

There are no specimens cited in the description of *S. flexicaule*; however, three separate specimens from Kew were collected during the voyage of the Sulphur in Guyaquil Ecuador. The Hinds and Sinclair collections are clearly the material that Bentham used when describing the species, making lectotypification and not neotypification necessary under article 9.11 of the ICBN (McNeill et al. 2006). Collections of *Barclay 520* were also collected during the Voyage of the Sulphur but the location on the original label on the BM collection is givens as Pasaje, Colombia, which

does not agree with the locality given in the protologue. The Hinds and Sinclair collections are very similar in appearance and it is possible that they are even branches of the same plant. The Hinds collection was chosen as the lectotype because he helped in preparation of the description and because the citation and page number for the publication "Bot. Sulph. p. 141" appear in Hinds' handwriting on the label.

Additional specimens examined. ECUADOR**. El Oro:** Pasaje, Oct 1836 (fl) *Barclay 520* (BM, US). **Guayas:** Cerca de Guayaquil (fl), *Ontaneda s.n.* (QPLS); Cerca de Puente de Chimbo, Sep 1891 (fl, fr), *Sodiro 140/47* (QPLS). **Los Rios:** Hacienda Clementina, Cerro Samama, trail between Destacamento Pita and La Torre, 1°39' S, 79°20' W, 600-700 m, 19 Sep 1999 (fr), *Gustafsson & Bonifaz 471* (NY); same loc., 25 Sep 1999 (fl, fr), *Gustafsson & Bonifaz 601* (NY); Hacienda Clementina, Cerro Samama, near Destacamento Pita on trail to Limón, 1°39' S, 79°20' W, 400-500 m, 14 Oct 2004 (fl), *Stähl & Andersson 6276* (NY); Jauneche, Estación Biologica Pedro Franco Dávila, Sur de la Carretera Quevedo-El Empalme, camino entre Mocache y Palenque entre Estero Maculillo y Estero Peñafiel, la division de las Cuencas de Río Daule y Río Babahoya a km 1 este del pueblo de Jauneche, 70 m, 7 Jul 1991 (fl), *Yánez & Foster 174* (QCA). **Probable specimen: Esmeraldas:** Quininde Cantón, Reserva Ecológica Mache-Chindul, Comunidad Caña Brava, cabeceras del Río Viche, estero Sabaleta, 00°25' N, 79°45' W, 250 m, 16 Mar 1998 (fl), *Clark 4663b* (NY).

Solanum jamaicense (6) Mill., Gard. Dict. ed. 8, no. 17. 1768. — TYPE: JAMAICA. *Houston s.n.* (Holotype BM! [000815972]).

Solanum brevipile Dunal in Poiret, Hist. Solan. 191, t. 21. 1813. As 'brevipilum'. — TYPE: WEST INDIES. *Reidle s.n.* (MPU).

Solanum cuneifolium Dunal, Hist. Solan. 193, tab. 22. 1813. — TYPE: FRENCH GUIANA. Cayenne, *sine coll. s.n.* (Holotype G-DC!; isotype P, Photo of holotype (F neg. 6835: F!), Photo of isotype (F. Morton neg. 8220: F!)

Solanum cuneifolium Willd. ex Roem. & Schult. Syst. 4: 623. 1819. — TYPE: PUERTO RICO. *Desfontaines* [label says "Riedle"] *s.n.* (Holotype B-W! 04387-010)

Solanum heterotricum Dunal, Hist. Solan. 192, tab. 20. 1813. As 'heterotrichum'. — TYPE: ?America, [*Forsythe*] *s.n.* (Lectotype, **here designated** G-DC; isotype P ex. herb Desvaux, MPU [fragment], Photo of lectotype [F neg. 6836: F!). [Fragm. Dunal 1813 at MPU fide D'Arcy, Fl. Pan.]

Names associated with this species that were not validly published: *Solanum croceum* Dunal Hist. Solan. 241. 1813. *Solanum acanthifolium* Léman ex Dunal, in A. DC., Prodr. 13(1): 255. 1852. *Solanum brevipilosum* Dunal DC. Prodr. 13(1): 199. 1852. *Solanum portoricense* Dunal in DC. Prodr. 13(1): 374. 1852. *Solanum umbellatum* Banks ex Dunal Gard. Dict. ed. 8 no. 27. 1768.

Shrub 1-2 m, occasionally scandent. Stems moderately armed with recurved, yellow to green roselike prickles, these 3-8 mm in length, the base 2-4 x 0.5-2 mm, moderately to densely pubescent with white, porrect-stellate hairs, the stalks nearly absent to 1 mm, multiseriate, the rays 6-8, 0.5-1mm, unicellular to multicellular, the midpoints absent to 1 mm. Flowering portions of the stem consisting of difoliate sympodial units, the leaves geminate, those of a pair unequal. Leaves simple, the blades 6-13x3-8 cm, rhombic, unlobed to 2-5 lobes per side, the sinuses cut less than 1/6 of the way to the midvein, the lobes obtuse, leaves chartaceous, slightly discolorous, dark green adaxially, light green abaxially, with both leaf surfaces sparsely to moderately pubescent with stellate hairs like those of the stem; major veins 3-6 on either side of the midvein,

the midrib abaxially unarmed or with occasional prickles like those of the stem; base acute, decurrent onto petiole; apex acute to obtuse; petioles absent to 1 cm, moderately pubescent with hairs like those of the stem, unarmed or occasionally armed with prickles like those of the stem. Inflorescenes 1-3 cm, extra-axillary, unbranched, with 5-15 flowers, apparently all perfect, the axes moderately to densely pubescent with hairs like those of the stem but with the stalks to 1.5 mm, unarmed; peduncle absent to 0.5 cm; rachis 1-3 cm; pedicels 5-10 mm in flower, 10-15 mm in fruit, filiform, nearly contiguous, spaced 0.5-1.5 mm apart. Calyx 2-7 mm long, the tube 1-2 mm, the lobes 3-5 x 0.5-1.5 mm, very narrowly triangular, moderately to densely pubescent with hairs like those of the stem but with the stalks to 1.5 mm, unarmed; fruiting calyx 4-9 mm, the lobes not accrescent in fruit. Corolla 1-2 cm in diameter, chartaceous, white to yellow-white, stellate, lobed nearly to the base, the lobes 4-6 x 1.5-3 mm, narrowly triangular, sparsely pubescent abaxially with hairs like those of the stem with midpoints either absent or to 1 mm, midpoints either white or occasionally purple, glabrous adaxially. Stamens 4-6 mm; filaments up to 1 mm, glabrous; anthers 3.5-5 x 1-2 mm, attenuate, tapering, connivent, yellow, the base cordate, the apex obtuse, the pores apical, directed introsely. Ovary very sparsely pubescent with multicellular, uniseriate glandular hairs 0.2-0.4 mm long; style 4-6 x 0.5-1.5 mm, exserted beyond stamens, cylindrical, white, sparsely pubescent with stellate hairs like those of the stem; stigma up to 1 mm wide, cylindrical, green. Fruit a thin-skinned berry, 4-12 mm in diameter, globose, mottled green when immature, mottled orange or red when mature, glabrous. Seeds 40-70 per fruit, 1-1.5 x 0.5-1 mm, reniform, brown, flattened, the surface netlike with many pits created by small raised ridges (Fig. 4.14).

Habitat and distribution. (Fig. 4.15) Weedy species of open fields, roadsides, or other disturbed areas from southern Florida through the Caribbean and Central America into northern South America and Brazil to northern Bolivia, at sea level to 900 m in elevation.

Etymology. The epithet refers to Jamaica, where the type collection was made.

Notes. *Solanum jamaicense* is the most widespread of the species in sect. *Eriophyllum* and is a very common weed in pastures and roadsides in lowlands throughout the range of the section. While it can become scandent on other vegetation in weedy tangles, it is also the most shrublike species within sect. *Eriophyllum*.

There are a number of characteristics of *S. jamaicense* that are unusual in the section. Although it is often scandent on other vegetation, *S. jamaicense* often has a more erect growth form that is uncommon in the section, which are normally vining. The rhombic leaves that nearly lack a petiole due to the decurrent leaf base are unique in the section. The flowers of *S. jamaicense* are among the smallest of the section and, although the anthers remain tightly connivent, the style is often bent at the apex. Additionally, *S. jamaicense* has small (4-12 mm in diameter), thin-skinned fruits that are mottled during development and calyx lobes with long-stalked stellate hairs.

Phylogenetic results of Stern & Bohs (in prep) place *S. jamaicense* sister to *S. lanceifolium*, although with only moderate support (71% BS, 1.0 PP) and places them sister to the remainder of section *Eriophyllum*. This sister relationship was somewhat unexpected as *S. lanceifolium* shares many morphological characteristics with *S. volubile,* which has been considered a synonym of the former (D'Arcy 1973). The small flowers and berries of *S. jamaicense* and *S. lanceifolium* are perhaps the most obvious shared characteristic between these species.

Solanum jamaicense has some of the most difficult nomenclatural issues in the section, likely due to its widespread distribution but also because many names, such as *S. acanthifolium* and *S. umbellatum,* were not published but instead were listed by Dunal as herbarium names. The name *S. brevipilosum* is an illegitimate name because in the publication *S. brevipilum* is listed as a synonym. This was likely an attempt to correct the original spelling of *S. brevipile*. D'Arcy (1973) cited the *P. Salzmann 384* specimen at G-DC as the lectotype for this species; however, this collection cannot be the lectotype because is not original material named in the 1813 description and the name is illegitimate since it had *S. brevipilum* listed in synonomy. A lectotype for this specimen should be chose from the Riedle collections at MPU, which were the basis for the original 1813 description. The name *S. heterotrichum* had two speciemens cited by Dunal. The speciemen at G-DC is lectotypified here because it has the best material.

Additional specimens examined. BELIZE**. Belize:** Sibun River, 1 mile in from mile 34.5 western highway, 5 Jul 1973 (fl), *Dwyer 11493* (F). **El Cayo:** Along Hummingbird at mile 28, 26 Jun 1973 (fl), *Dwyer 11414* (F). **Toledo:** W of Punta Gorda on road from Punta Gorda to San Jose, 3 Aug 1970 (fl), *Wiley 32* (F).

BOLIVIA**. Beni:** Prov. Cercado, vicinity of campus of the Universidad Tecnica del Beni, 2.5 km N of center of Trinidad, 14°48'S, 64°53'W, 26 Feb 1987 (fl, fr), *Nee 34265* (US). **Pando:** Manuripi, Conquista, Embarcadero sobre el Madre de Dios, 150 m, 3 Feb 1983 (fl, fr), *Casas 8597* (G) **Santa Cruz:** Prov. Velasco, Reserva Ecologica El Refugio, a 300 m al E del acampamento Toledo sobre el camino hacia el Río Paragua, 14°42'33" S, 61°09'19" W, 200 m 16 May 1995 (fr), *Guillen & Medina 3703* (F).

BRAZIL**. Amapa:** Rio Matapi desde a Estrada até a foz do rio-Macapá, 4 Mar 1983 (fl), *Rabelo et al. 1856* (K) **Amazonas:** Outskirts of Leticia along road to

Tabutinga, 200 m, 12 Mar 1977 (fl, fr), *Gentry & Daly 18223* (F); Municipality São Paulo de Olivença, near Palmares 11 Sep- 26 Oct 1936 (fl, fr), *Krukoff 8044* (BR, F, G, K, USMunicípio de Marã, Rio Japurá, sítio Cuiú-cuiú, aprox. 2°28'S, 65°03'W, 3 Dec 1982 (fl, fr), *Plowman et al. 12147* (F, K, US); Prope San Gabriel de Cachoeira, ad Rio Negro, Jan 1852 (fl), *Spruce 2104* (F); **Bahia:** km 40-41, BR324, 21 Dec 1982 (fl, fr), *Nobick et al. 2523* (F); in convorllibus, 1831 (fl, fr), *Saltzmann sn* (BR, G). **Maranhão:** Viana, 20 May 1918 (fl), *Carvalho 2107* (US). **Pará:** Estacão do Jari, projecto reserva genetica, SEMA, 00°75'S, 52°30'W, 13 Oct 1987 (fl), *Beck et al. 75* (K). **Pernambuco:** Tapéra, 1 Jan 1930 (fl, fr), *Pickel 2253* (US). **Rondonia:** Mun. Porto Velho, along hwy. BR 364 at Corrego Raiz, 21 km. ENE of junction with hwy. BR 325, 22 km (by air) E of Abuna, 9°43'S, 65°10'W, 140 m, 18 Mar 1987 (fl, fr), *Nee 34931* (F, K, US).

COLOMBIA**. Amazonas:** Road west of Leticia, 2 Jul 1967 (fl), *Plowman & Martin 127* (F, US); Río Putomayo, carretera entre Caucaya (Puerto Leguizamo) y La Tagua, 225 m, 17 May 1942 (fl), *Schultes 3893* (F). **Antioquia:** Mun. de Valdivia, Corregimiento Puerto Valdivia, margen derecha de la quebrada Valdivia, 7°21' N, 75°22' W, 60 m, Feb 2000 (fr), *Fonnegra et al. 7276* (F). **Bolivar:** Boca Verde, 100-300 m, 13-14 Feb 1918 (fl), *Pennell 4218* (US). **Caldas:** Barancas, Río Samana, 600 m, 26 Jul 1965 (fl), *Barkley & Gutierrez 35355* (F). **Caquetá:** Florencia, Jan 1946 (fl), *Camilo 65* (F). **Cesár:** San Alberto, Plantación-Bloque E8, industrial agraria La Palma, 11 Mar 1981 (fl), *Garzón S-2* (G). **Chocó:** Río San Juan, orilla izquierda, quebradita frente a Palestina, 0-5 m, 28 May 1946 (fl), *Cuatrecasas 21387* (US); Andagoya, 70-100 m, 20-30 Apr 1939 (fl, fr), *Killip 35057* (US). **Cudinamarca:** La Palma, carretera a Pacho, Río Murca, 1150-1400 m, 29 Jul 1947 (fl), *Garcia-Barriga 12411* (US). **Huila:** Km 9 from Pitalito to San Agustin, 17 Aug 1974 (fr), *Plowman & Davis 4163* (F). **Los Llanos:** Río Meta, Orocué,

140 m, 16 Oct 1938 (fl, fr), *Cuatrecasas 3714* (US). **Magdalena:** Santa Marta, near sea level, 1898-1901 (fl), *Smith 1146* (BR, F, G, US). **Meta:** Puerto López, 300 m, 29-30 Jul 1946 (fl), *Jaramillo et al. 384* (US). **Putomayo:** San Pedro, between Umbria and Puerto Asis, 250 m, 28 Nov 1968 (fl, fr), *Plowman 2085* (F, US). **Santander:** Vicinity of Puerto Berrio, between Carare and Magdalena rivers, 100 m, 31 Jul 1975 (fl), *Haught 1975* (F, US). **Valle del Cauca:** Cerca al Puente G. Vakancia, sobre el Río Cauca, 1000 m, 3 Sep 1968 (fr), *Espinal 2531* (F); Samaria, on Río Timba, 2 km W of Timba, 3°06' N, 76°40'W, 1000 m, 13-14 Apr 1943 (fl, fr), *Fosberg 20501* (US); Río Timbio, 1200 m, 16 Sep 1938 (fl), *Sneidern 2579* (F, US); Cali, 1003 m, 1 Nov 1972 (fl), *Zorello & Espuusa 17* (F). **Vaupes:** Bajo Vaupes, Mitu y sus alrededores, Mar 1944 (fl), *Guitierrez & Schultes 1025* (F).

COSTA RICA**. Alajuela:** On road to Laguna Hule, 10°17' N, 84°12' W, 900 m, 11 Mar 1973 (fl), *Lent 3259* (F); Cantón San Carlos, Villa Quesada, 825 m, 14 Mar 1939 (fl), *Smith 1757* (F). **Cartago:** Valley of Tio Reventazon, 9 km. ENE of Turrialba near Pavones, 30 Jun 1949 (fr), *Holm & Iltis 201* (F, G, K). **Guanacaste:** Parque Nacional Santa Rosa, 10°57' N, 85°36' W, 100 m, Jul 1983 (fl, fr), *Barringer et al. 4063* (F). **Heredia:** Finca La Selva, the OTS Filed Station on the Río Puerto Viejo just E of its junction with the Río Sarapiqui, 100 m, 13 Feb 1981 (fl), *Folsom 8941* (F); Cantón de Sarapiquí, Rara Avis, ca. 15 km al suroeste de Horquetas, entrada a El Plastico y camino El Tigre, 10°17' N, 84°02' W, 400 m, 400 m, 22 Sep 1989 (fl, fr), *Vargas 165* (F). **Limón:** Matina, P.N. Barbilla, Cuenca del Matina, sector Colonia Puriscaleña, sendero Cerro Azul, 9°59'44"N, 83°23'08"W, 500 m, 9 Apr 2000 (fl, fr), *Mora 991* (G). **Puntarenas:** Along Río Sonador near Panamerican Highway, El General Valley, 600 m,

31 Jan 1965 (fl), *Wilson 28745* (F). **San José:** Vicinity of El General, 610 m, Feb 1939 (fl, fr), *Skutch 3926* (K).

CUBA**. Camaguey:** vicinity of La Gloria, 2 Feb 1909 (fl, fr), *Shafer 223* (US). **Habana:** Near Laguna de Ariguanabo, Anafe, 2 Jan 1914 (fr), *Bro. León 4199* (US). **Isla de Pinos:** In swamp 2 km N of Nueva Gerona, Isla de Pinos, near sea-level, 6-10 Feb 1956 (fl, fr), *Morton 10000* (US). **Maranzas:** Jaguey Grands, 22°05'N, 80°30'W, 3 m, 15 Nov 1988 (fr), *Dechamps & Carrera 12161* (BR). **Oriente:** San Jose, Sierra de Nipe, Jul 1941 (fr), *Howard 6198* (US). **Pinar del Río:** Mantua to Arroyos, 28 Dec 1911 (fl), *Shafer 11235* (US). **Santa Clara:** Dist. of Cienfuegos, Cienquita, 6 Nov 1895 (fr), *Combs 190* (K).

ECUADOR**. Esmeraldas:** 2-4 km SE of San Lorenzo, 1°15' N, 78°50' W, 10 m, 7 Oct 1983 (fl), *Boom 2516* (F, US); El Nadadero near San Lorenzo, 28 Jul 1963 (fl, fr), *Játiva & Epling 599* (US).

FRENCH GUIANA**. No Dept:** Saül, vicinity of Eaux Claires, Sentier Botanique, from entrance to 260 m from entrance, 3°37' N, 53° 12' W, 200-400 m, 30 Oct 1992 (fl, fr), *Mori et al. 22716* (US); Lieu-dit Maya, route de la Carapa, Macouria, 4°56'59"N, 52°26'30"W, 9 m, 6 Oct 2005 (fl, fr), *Tostain et al. 825* (US); Along road between ferry and Roura, +/- 1 km from ferry, 4°43' N, 52°20' W, 50 m, 12 Sep 1987 (fl, fr), *Weitzman & Hahn 252* (US).

GUATEMALA**. Alta Verapaz:** Near Secanquin, trail to Cahabon, 25 Nov 1904 (fr), *Goll 29* (US). **Izabel:** Los Amates, 160 ft, 6 Feb 1905 (fl, fr), *Bartlett 259* (US); Village of Izabel, 30 Apr 1966 (fr), *Jones et al. 3194* (F, US); Between Cienaga and Ceja, along the Peten- Rio Dulce highway, 13 Mar 1972 (fl, fr), *Ortiz 2372* (F, US); 2.5 miles W of Cubilguitz, 250 m, 28 Feb 1942 (fl, fr), *Steyermark 44240* (F). **Petén:** Santa Elena, km 4

of Poptun road, 7 May 1966 (fl), *Contreras 5690* (F, US); Machaquila, km 77, road beyond Poptun, 13 Jul 1959 (fl), *Lundell 16400* (F).

GUYANA**. Cuyuni-Mazaruni:** Approx. 100 m below Eping Landing, opposite confluence with Perenang Creek, 06°05'N, 60°07' W, 76-122 m, 15 Nov 1990 (fl, fr), *McDowell 3788* (US). **Demerara-Mahaica:** East Coast Demerara, Cane Grove Conservancy, Flagstaff, 6°38' N, 57°56' W, sea level, 19 Feb 1989 (fl), *Gillespie & Tiwari 701* (US). **East Demerara:** C.A.S. Mon Repos, 29 May 1958 (fl, fr), *Harrison 951* (K); Ituni Road, Mackenzie, 1 Jun 1945 (fl, fr), *Fanshawe 5230* (K). **Essequibo:** Bonasika-Boerasine, 2 Sep 1920 (fl, fr), *Rambaran 51* (K). **Essequibo Ils-W. Demerara Region:** Area W of Demerara River, N and S of Wales, 6°40' N, 58°11' W, 1 m, 4 Dec 1986 (fl), *Pipoly & Ameer 9114* (US). **Mazaruni:** Mazaruni Station, 12 Aug 1937 (fl, fr), *Sandwith 1032* (K). **Potaro-Siparuni Region:** Garraway Stream, 102.5 miles on Bartica-Potaro Road, 5°22'25.2"N, 59°07'20.5W, 38 m, 13 Mar 2004 (fr), *Redden et al. 2279* (K, US). **West Demerara:** West Bank Demerara River, 6°50' N, 58°25' W, sea level, 7 Apr 1987 (fl, fr), *Boom 7195* (US); Parika backdam, 06°50' N, 58°28' W, 0-10 m, 18 Aug 1993 (fr), *Henkel et al. 2670* (US). **No Loc:** Demerara-Mahaica Region, along road from Cane Grove to Lama Conservancy, 6°35'N, 57°50'W, 1-10 m, 10 Feb 1988 (fl, fr), *Hahn et al. 3814* (K, US); E. Berbice-Corentyne, Canje Creek, 10-25 km upriver from mouth, 6°00' N, 57°20' W, sea level, 28 Aug 1992 (fl, fr), *Hoffman 2426* (US); Georgetown, in Botanic Garden, 5 Nov 1919 (fl), *Hitchcock 16624* (US); East-Berbice-Corentyne Region, S Awara Savanna, 35 mi S of Torani Canal, on Canje R., 3 mi SE of Digitima Creek, 5°43'N, 57°32'W, 1-25 m, 18 Dec 1986 (fr), *Pipoly 9399* (K, US).

HONDURAS**. Atlantida:** A orillas de la Estacion Experimental de Lancetilla, 20 m, 16 Mar 1962 (fl), *Molina 10297* (F, US). **Colón:** Cerro Capiro y Calentura, 3 km al SE de

Trujillo, 200 m, 29 Sep 1989 (fr) *Duron 63* (F). **Comayagua:** Cerca de Santa Cruz de Yojoa, area Lago Yojoa, 500 m, 31 Mar 1963 (fl), *Molina 11813* (F). **Morazán:** Vicinity of El Zamorano, near Casa Grande, 800 m, 22 Sep 1948 (fr), *Standley 12562* (F). **Olancho:** Trail between Catacamas and La Presa, north of Catacamas, 500 m, 20 Mar 1949 (fl), *Standley 18568* (F). **Yoro:** Vicinity of Paya, Río Paya, along trail from Paya to Pucro (fl), *Stern 219* (F, G, US).

MEXICO**. Chiapas:** Mun. Ocosingo, 300 m, 16° 07' N, 90° 55' W, 8 Oct 1991 (fr) *Domínguez 109* (fr). **Oaxaca:** Near Santo Domingo, 1600 ft, 18 Jun 1895 (fl, fr), *Nelson 2711* (US). **Veracruz:** Mun. Mecayapan, in saddle between Volcán Santa Marta nad Volcán San Martin Pajapan, 7.5 km (by road) NE of Tatahuicapan on dirt road to Benigno Mendoza, 18°19' N, 96°46' W, 300 m, 16 Jul 1982 (fl), *Nee et al. 25104* (F).

NICARAGUA**. Atlantico Sur:** Finca Santa Rosa, ca. 2.5 km ENE of Rama, 0 m, 8 Apr 1966 (fl, fr), *Proctor et al. 27394* (F, US). **Chontales:** Vicinity of La Libertad, 500 m, 29 May 1947 (fl), *Standley 8833* (F). **Zelaya:** Jackson Farm W of Bluefields, 0 m, 3 Mar 1971 (fl), *Nelson 4123* (F).

PANAMA**. Canal Zone:** Barro Colorado Island, near Lighthouse Clearing, 7 Sep 1970 (fl, fr), *Croat 11987* (F). Gamboa Naval Reservation, 15 Aug 1960 (fl), *Ebinger 897* (F, US); Along road K-10, 4 km N of Arraijan, 115 m, 27 Sep 1973 (fr), *Nee 7162* (US); Agua Clara, on the Trinidad River, 10 m, 19 Jul 1911 (fl), *Pittier 3979* (F, US). **Colón:** Alrededores de Palmas Bellas, 20 May 1971 (fl), *Thoms 30* (F) **Darien:** Between Paya and Palo de los Letras, 30 Aug 1967 (fr), *Duke & Kirkbride 14039* (US); **Herrera:** Road between Las Minas and Pese, ca. 600 ft., 14 Jul 1967 (fr), *Duke 12316* (US). **Panama:** Ancón Hill, 22 Sep 1917 (fr), *Killip 3030* (US); Near Tapta River, Juan Diaz

region, 1 Jun 1923 (fl), *Maxon & Harvey 6737* (F, US). **Veraguas:** Altos de Campana, 300 m del Motel Sulin, 930 m, 11 Jun 1977 (fl), *Mendez 26* (F).

PERU**. Loreto:** Outskirts of Iquitos, near Primate Center, 22 Jun 1981 (fl), *Bohs 1525* (F); Maynas, outskirts of Iquitos, 120 m, 8 Jan 1976 (fl), *Gentry et al. 15756* (F); Maynas, Río Momon, tributary of Río Nanay, near Iquitos, 130 m, 23 Oct 1980 (fr) *Gustafson 1955* (F); Maynas, Río Yaguasyacu, affluent of Río Ampiyacu, Brillo Nuevo and vicinity, 2°40' S, 72°00'W, 5 May 1977 (fl, fr), *Plowman et al. 7264* (F, US); Maynas, Iquitos, Pto. Almendras, 3°48' S, 73°25' W, 122 m, 30 Dec 1987 (fl, fr), *Vásquez & Jaramillo 10252* (F); Caballo-cocha on the Amazon River, Oct 1929 (fl), *Williams 2180* (F).

SURINAME. **No Dept:** Mar 1842 (fl, fr), *Hostmann 220* (F, G, M); Prope stationem Victoriam in reg. inter. ad fl. Surinam, Dec 1843 (fl, fr), *Kappler 1348* (G, G, W, W); Paramaribo (fl, fr), *Wullschlägel 367* (BR, W).

VENEZUELA. **Barinas:** Dtto. Pedraza, Progresiva 3 + 150, zona de transicion banco-bajio, Pcia C-V-a, boca del Uribante, norte Franco 19 kms, pasando 5 kms mas alla del Cano Aranu, 19 Jan 1978 (fl), *Trujillo et al. 14590* (F). **Bolivar:** Mun. Aeres, Finca Monserratte, 2 Apr 1990 (fl), *Tillett et al. SPB607* (US). **Carabobo:** Alrededores de Campo Carabobo, 400 m, 7 Sep 1968 (fl, fr), *Benitez 462* (F). **Distrito Federal:** Carnao valley, 15 Jul 1925 (fl), *Pittier 11839* (G, US). **Falcon:** Between Valencia and Campanero, 900 m, 7 Mar 1857 (fl), *Fendler 993* (F). **Miranda:** Parque Nacional Guatopo, near park headquarters at south entrance, 13 Feb 1973 (fl), *Croat 21723* (F). **Monages:** 1-2 km S of La Pica along road to Laguna Grande, 12 km ENE of Maturin, 40 m, 13 Aug 1979 (fl), *Nee 17448* (F). **Nirgua:** Edo. Yaracuy, Vertiente Norte de la Selva Nublada, 1100 m, 3 Jun 1978 (fl), *Benitez de Rojas 2232* (G). **Tachira:** Dist. Jáuregui,

Mun. J.T. Colmenares, potrero La Sabana y Jabilla, Hacienda La Honda, cerca de Coloncito, 120 m, 3 Sep 1967 (fl), *Steyermark & Velasco 99994* (US). **Sucre:** En solares de Los Altos, Jan 1942 (fl), *Tamayo 2164* (US). **Zuila:** Mun. Jesús María Semprún, sector Los Manueles, 10-15 km al NE de Casigua El Cubo, 8°49'N, 72°29'W, 30-60 m, Nov 2001 (fr), *Fernández 17925* (US).

WEST INDIES. **Dominican Republic:** Alto de Miches, between El Seibo and Miches, Prov. El Seibo, 25 Mar 1970 (fl), *Julia & Jiménez 5791* (US); Prov. Monte Cristi, Lagunas de Cenobí, Dist. of Sabaneta, 18 Aug 1929 (fl, fr), *Valeur 31* (US). **Grenada:** On Mt. Felix, 1500 ft, Nov 1889 (fl, fr), *Eggers 6055* (US). **Isla de Pinos:** Near Nueva Gerona, 26 Dec 1903 (fl, fr), *Curtiss 258* (G, K, M, US). **Jamaica:** Town, Cinchona Plantation (fl, fr), *Hart 561* (US); Moneagua, Jan-Aug (fl, fr), *Prior 67* (K); Windsor House estate, 400 ft, 11 Mar 1956 (fl, fr), *Stearn 471* (K). **Martinique.** Environ de Fort de France, 1873 (fl), *Hahn 625* (G, G); In Nord, La Lovrain, 120 m, 29 Dec 1941 (fr), *Stehlé 4997* (US). **Puerto Rico:** Cerro Pandura, Santa Elena, 500 m, (fr), *Alain 30958* (US); Caroliná, 18 Feb 1914, (fl, fr), *Johnston 1378* (US); Sierra de Naguabo, Loma Icaco, 210-675 m, 24 Jul 1914 (fl, fr), *Shafer 3429* (US); Santa de Luquillo, in monte Jimenes, 21 Jun 1885 (fl, fr), *Sintenis 1680* (G, K, M, US). **St. Lucia:** Marc Dist. above Crown Lands, SW of Piton Flore, 300-1000 ft, 4 Apr-12 Jun 1958 (fl), *Proctor 17604* (US). **Trinidad:** Nariva Swamp 46 milepost, sealevel, 7 Dec 1961 (fr), *Aitken 25* (K); Tabaquito Rio Claro Road, 4.5 milepost, 19 Jul 1926 (fl), *Broadway 6341* (K).

Solanum lanceifolium (7) Jacq., Coll. 2: 286. 1789. Ic. Pl. Rar. 2: 11, tab. 329. 1787. As "*lanceaefolium*". — TYPE: WEST INDIES. *P. Isert s.n.* (Lectotype W! [W0022641] ex herb. Jacquin (designated by D'Arcy 1970); isolectotypes BM!, W! [W0022640], photo of lectotype (F neg. 33085: F!, MO!)

Solanum ambiguum Dunal, Solan. Syn. 32. 1816. [193]. — TYPE: No location but probably West Indies, 1815, *Thibaud s.n.* (Holotype G-DC! [G00145860]; isotype P, photo of holotype (F neg. 6824: MO!))

Solanum brachyacanthum Dunal, Solan. Syn. 32. 1816. *Solanum lanceifolium* Jacq. var. *brachyacanthum* (Dunal) O. Schulz, in Urban, Symb. Ant. 6: 247. 1909. — TYPE: VENEZUELA. Edo. Sucre, Cumaná, Mt. Cocollar, 480 hex., Sep 1799, *A. Humboldt & A. Bonpland s.n.* (Holotype P-HBK!; isotypes B-W! [04408-010], P, photo of holotype (F neg. 38992: F!), photo of B-W isotype (F neg. 18390: F!)).

Solanum crotonoides Sieber ex Presl, Bot. Bemerk. 101. 1845. TYPE: MARTINIQUE. *F. Sieber 66* (lectotype, **here designated** W[293730]; isolectotypes BM [BM000886695], BR!, BR!, G-BOIS= F photo 34112 M [M-0142758], MO! [MO-2873376], W [W0003292])

Solanum calvefactum Dunal, in A. DC., Prodr. 13(1): 226. 1852. —TYPE: MARTINIQUE. *F. Sieber 66* (Holotype G-BOIS!, =F photo 34112; isotypes BR!, BR!, L! [908246-267], M! [M-0142758], MO! [MO2873376], W! [0003292], W! [293730]).

Solanum lanceifolium Jacq. var. *punctato-maculatum* Dunal in A. DC. Prodr. 13(1): 221. 1852. [536]. — TYPE: TRINIDAD. 1826, *Sieber 132* (Holotype G-DC! [G00145856]; isotypes F! [F-680232], F! [F-875753], MO! [MO-2873382], P, W! [W193010], W! [0003507], W! [16936], W! [293734], photo of holotype (Morton neg. 8442: MO!), photo of P isotype (Morton neg. 8233: MO!)

Solanum enoplocalyx var. *mexicanum* Dunal, in A. DC. Prodr. 13(1): 222. 1852. [537]. —TYPE: MEXICO. Tampico de Tamaulipas, 1827, *Berlandier 48* (Holotype G-DC! [G00145855]; isotype G!, P)

Names associated with this species that were not validly published: *Solanum inaequale* K. Presl, Bot. Bemerk. 101. 1845. *Solanum obscurum* Sieber ex Dunal, in A. DC. Prodr. 13(1): 224. 1852. *Solanum preslei* A. DC. ex Dunal, in A. DC., Prodr. 13(1): 681. 1852.

Vine, 1-4 m. Stems moderately armed with recurved, tan roselike prickles, these 1-2 mm long, the base 1-2 x 0.5-1 mm, densely pubescent with white to tan , porrect-stellate hairs, the stalks nearly absent to 1 mm, multiseriate, the rays 5-8, 0.5-1 mm, unicellular to multicellular, the midpoints nearly absent to 0.5 mm. Flowering portions of the stem consisting of difloiate sympodial units, the leaves geminate, those of a pair slightly unequal. Leaves simple, the blades 3-7 x 1-3 cm, ovate, chartaceous, slightly discolorous, dark green adaxially, light green abaxially, both leaf surfaces moderately to densely pubescent with hairs like those of the stem but with the midpoints 0.5-1 mm; major veins 3-6 on either side of the midvein, the secondary veins obscure, the midrib abaxially with a few to many recurved pirckles like those of the stem; base acute, often asymmetrical; margin unlobed; apex acute; petioles 0.5-2 cm, with recurved prickles like those of the stem. Inflorescences 2-3 cm, extra-axillary, unbranched, with 5-15 flowers, apparently all perfect, the axes moderately to densely pubescent with hairs like those of the stem, unarmed; peduncle 0.5-1.5 cm; rachis 1.5-2.5 cm; pedicels 5-10 mm in flower, 10-30 mm in fruit, filiform, expanded distally, spaced 1-3 mm apart. Calyx 2-4 mm long, the tube 1-2 mm, the lobes 1.5 x 0.5-1 mm, the lobes often reflexed, narrowly triangular, moderately to densely pubescent with hairs like those of the stem, unarmed fruiting calyx 3-5 mm, not accrescent in fruit. Corolla 1-2 cm in diameter, chartaceous, white, stellate, lobed nearly to the base, the lobes 5-10 x1-3 mm, lanceolate, moderately pubescent abaxially with hairs like those of the stem, nearly glabrous adaxially. Stamens 6-7 mm;

filaments 1-2 mm long, glabrous; anthers 5-6 x 1-2 mm, attenuate, tapering connivent in bud, connivent to spreading in flower, yellow, the base cordate, the apex obtuse, the pores apical, directed slightly introrsely. Ovary glabrous; style 6-9 x 0.5-0.75 mm, exserted beyond stamens, cylindrical, white, glabrous; stigma 0.5-1 mm wide, green. Fruit a thin to leathery skinned berry, 8-14 mm in diameter, globose, green when immature, orange to dark red when mature, glabrous. Seeds 15-25 per fruit, 2-2.5 x 1.5-2 mm, reniform, brown, flattened, the surface netlike with many pits created by small raised ridges (Fig. 4.16).

Habitat and distribution. (Fig. 4.17) In disturbed areas and forest gaps from central Mexico through Central America and the Caribbean into northwestern South America at 100 -1600 (2900) m.

Etymology. The epithet refers to the lance-shaped leaves of the species.

Notes. The concept of *S. lanceifolium* presented above is a broad definition and encompasses much morphological variability. If one were to look at two specimens of *S. lanceifolium* there is a great likelihood that they would question whether they belong to the same species due to the great range of phenotypes in the species. However, drawing boundaries between phenotypes is nearly impossible due to the continuous variability of characters. Some of the most obvious differences in many collections are leaf size and pubescence. Leaves of many of the Mexico and Central America specimens are small with abaxial surfaces that are so densely pubescent that the mesophyll is not visible. Specimens from the Caribbean islands often have much larger leaves that are very sparsely pubescent which likely led to these being named as *S. lanceifolium* var. *litorale*. Because these phenotypic differences are continuous, it is not possible to draw boundaries and differentiate these as distinct species.

One example of local variation includes collections from Dominica, such as *Whitefoord 7021* (BM) and *Nicolson 2163* (MO), that have large leaves (to 15 x 5 cm) that are thinner and less pubescent than normal. However, other specimens from the Caribbean have large, densely pubescent leaves and some Central American specimens (notably some of the higher elevation collections from Nicaragua) have very large, sparsely pubescent leaves. The presence of these intermediates on the spectrum makes it necessary for me to "lump" these seemingly disparate phenotypes under a broad species concept.

The best characters to define *S. lanceifolium* are the presence of many small (1-2 mm long), broad-based, recurved prickles on the stem, the filiform pedicels that expand distally, especially in fruit, the small flowers with corollas 1-2 cm in diameter, and the generally small (3-7 x 1-3 cm), unlobed, membranaceous leaves that are moderately to densely pubescent below.

The lectotype of *S. lanceifolium* was a collection made by Isert in his 1787 trip to the West Indies that Jacquin saw for his 1789 description. The specimen at W was annotated by Jacquin and designated as the lectotype by D'Arcy (1970). This specimen is particularly nice because it is intermediate in many of the characteristics, such as leaf size and pubescence, that would at first glance appear to separate the Caribbean and Central American specimens. The type has slightly wider and more sparsely pubescent leaves than some Central American specimens but they are not as wide and are more pubescent than many Caribbean specimens.

We have lectotypified *S. crotonoides* with the specimen at W because it has the best material but this name was previously used by Lamarck in 1794. The name *S. obscurum* is a herbarium name that was used but never validly published. *Solanum*

preslei was also not validly published because it names *S. crotonoides* and *S. inaequale* as synonyms. The name *S. inaequale* was previously used by Hornemann in 1819 for a member of *Solanum* section *Torva* and then was used by Vellozo in 1829 for a species in *Solanum* section *Geminata* making it an illegitimate name.

Additional specimens examined. BELIZE**. Cayo:** Arenal, Jun-Aug 1936 (fr), *Lundell 6161* (US); Las Cuevas Research Station, grid ref WG584, 16°44.01'N 88°59.14'W, 590 m, 27 Jun 2000 (fl, fr), *Smith 34* (BM); S. of Guacamallo Bridge, Chiquibul Road, 9 May 1981 (fr), *Whitefoord 2813* (BM).

COLOMBIA**. Caldas:** La Paila, valle du Cauca, 1851-1857 (fl), *Triana 1866* (G). **Cudinamarca:** Entre Pacho y Río Negro, carretera y alrededores, 1000-1200 m, 22-26 Feb 1942 (fr), *Garcia-Barriga 10736* (US). **Cauca:** Mercaderes, 1100 m, 29 Oct 1946 (fl, fr), *Haught 5149* (US). **El Valle:** Cauca Valley, 1 Sep 1922 (fr), *Killip & Hazen 11053* (US). **Magdalena:** Alto Río Buritaca, Alto de Mira, por el camino a la Cascada del Caño Negro, 11°05'N, 73°48'W, 1000-1100 m, 14 Jul 1989 (fl), *Madriñán & Barbosa 240* (GH); Parque Tairona, Canaveral, trail to Arrecifes, 100 ft, 20 May 1974 (fr), *Plowman & Davis 3717* (GH, K). **Norte de Santander:** Chinaota, 1300 m, 16 Feb 1876 (fl), *André 1623* (K). **Quindio:** Quindio, Páramo, 2900 m, Jan 1853 (fl), *Triana 3855-28* (BM). **Tolima:** Girardot, El Espinal, matorrales en quebrada del Enial, 400 m, 13 Jun 1939 (fl), *Arbeláez & Cuatrecasas 6535* (US). **Valle de Cauca:** Cordillera Occidental, variente occidental, hoya del Río Sanquininí, loma con matorrales en Naranjal, 1200 m, 8 Dec 1943 (fr), *Cuatrecasas 15339* (F, US). **No dept:** Entre Cartago and Naranjo, 25 Mar 1896 (fl), *André 2598* (F, K); Paramo de Quindio, 2700 m, 1851-1857 (fl), *Triana 2229* (BM, G, W).

COSTA RICA. **Alajuela:** Cantón de San Ramon, Cordillera de Tilarán, entre San Isidro y Palmares, Cerro Piedra Grande, 10°04'55"N, 84°27'00"W, 1200 m, 30 Apr 1995 (fr), *Hammel et al. 19804* (BM); Beginning of trail toward river, Alajuelita, south of San José, 28 May 1955 (fl), *Schubert & Rogerson 628* (A). **Cartago:** Alto de Ochomogo, 1550 m, Dec 1896 (fl), *Cendrez 10405* (US); Linda Vista Lmda. farm in Dulce Nombre de Cartago, 1300 m, 12 Mar 1967 (fl), *Lent 750* (F); Upper part of the river trail near Alajuelita, south of San José, 7 Jun 1955 (fl), *Schubert & Rogerson 659* (A); 1 mi. W. of Cartago, 4700 ft., 11 Jun 1932 (fr), *Stork 2871* (F). **Guanacaste:** Entre Tilarán y El Silencio, 680 m, 12 Feb 1963 (fl, fr), *Jiménez 373* (F); Just west of Tilarán, Cordillera del Guanacaste, 3 Jan 1964 (fl), *Williams, et al. 26581* (F). **Puntarenas:** Jan 1854 (fl), *Scherper s.n.* (W) **San José:** Haies a San Francisco de Guadelupe, May 1894 (fl), *Tonduz 8769* (BR); San José, 1160 m, Apr 1932 (fl, fr), *Valerio 155* (F).

FRENCH GUIANA. 1792 (fr), *Leblond 364* (G).

GUATEMALA. **Baja Verapaz:** Pauzal, 1000 m, Apr 1907 (fl, fr), *Türckheim 1750* (US). **Guatemala:** Arrazola, 6000 ft, May 1892 (fl), *Heyde et Lux 3447* (GH, K, US). **Petén:** Uaxactun, 6 Apr 1931 (fr), *Bartlett 12478* (A, US); In ramonal covering the ruins, on sawmill-east, Tikal National Park, Tikal, 13 Mar 1966 (fl, fr), *Contreras 5569* (BM, G); El Paso, 9 Apr 1932 (fl), *Lundell 1465* (F); Tikal, block 4F, south of aguada, 1 Feb 1959 (fl), *Lundell 15271* (F).

HONDURAS. **Atlantida:** Valley near dam for water supply of Progreso, 12 Aug 1929 (fr), *Bangham 366* (A, F). **Cortés:** La Montaña La Zona, canon del Río Piedras, 3 kms de San Pedro Sula, 190 m, 28 Nov 1950 (fl, fr), *Molina 3406* (F, GH). **Morazán:** Entre la quebrada Tarán y Valle de Angeles, 1300 m, 3 Aug 1962 (fr), *Molina 11097* (F); Zamorano, 800 m, Aug 1944 (fl), *Rodriguez 206* (F); Near Suyapa, 1200 m, 25 Nov-14

Dec 1946 (fr), *Standley & Williams 505* (F); Vicinity of El Zamorano, 780-900 m, 17 Feb-8 Mar 1947 (fl), *Standley 4985* (F). **Olancho:** A lo largo de la carretera cerca de Río El Boquerón, 300 m, 19 Nov 1963 (fl, fr), *Molina 13256* (F, GH, US).

JAVA**:** Lawang Bot. Garden, 15 Feb 1913, (fl), *M. Brijsman* (K).

MEXICO**. Campeche:** En los alrededores de la Zona Arqueológica de Becan, aprox. 5 km al O de Xpujil, por al carr. Chetumal-Escárcega, 19 May 1985 (fr), *Cabrera et al. 8412* (BM); En las inmediaciones de la Zona Arqueológica de Chicana, 15 Feb 1988 (fr), *Cabrera & Cabrera 15527* (GH). **Chiapas:** 17 miles east of La Trinitaria along road to the Lagos de Montebello, Municipio of La Trinitaria, 5000 ft, 26 Jul 1965 (fr), *Breedlove 11320* (F). **Colima:** Road-summit, 8 miles west-northwest of Santiago, road to Cihuatlán, Jalisco, 135 m, 25-26 Jul 1957 (fl), *McVaugh 15761* (G). **Michoácan:** Coalcomán, San José, 900 m, 22 Jun 1939 (fl), *Hinton et al 13832* (F, GH, W). **Nayarit:** Tres Marias Islands, Maria Madre Island, 3-25 May 1897 (fr), *Nelson 4240* (F, GH). **San Luis Potosi:** 8 miles east of Valles, 9 May 1948 (fl, fr), *Kenoyer & Crum 3886* (A); Near Los Canos, 15-21 Oct 1902 (fl, fr), *Palmer 275* (BM, F, GH); E. slope of Sierra Madre Oriental 48 km W of Valles on highway 86, 21°55'N, 99°20'W, ca. 1000 m, 30 Sep 1965 (fr), *Roe & Roe 2260* (BM). **Tamaulipas:** Across from a gravel pit, on route B-5, 3 miles east of Gomez Farias, in Municipio Gomez Farias, 600 ft, 31 Mar 1975 (fl, fr), *Harriman 10687* (F); Vicinity of Tampico, about 15 m, 1-31 Jan 1910 (fl, fr), *Palmer 84* (A, BM, F, G, GH, K). **Veracruz:** Mun. Pueblo Viejo, Ejido González Ortega, 21°50'N, 98°03'W, 125 m, 2 Mar 1980 (fr), *Avendaño et al. 619* (F); Mun. Tempoal, El Mirador, Presa Paso de Piedras, 21°31'N, 98°07'W, 40 m, 6 Sep 1980 (fl, fr), *Calzada et al. 6226* (F); Mun. Tepetzintla, Sierra de San Juan Otontepec, 21°13'N, 97°55'W, 500 m, 13 Dec 1981 (fl, fr), *Castillo, Nee, & Benavides 2438* (F); A 2 km de Ozuluama, por el camino a la Laja

Ozuluama, 21°39'N, 97°49'W, 7 Dec 1960 (fr), *Chiang 231* (BM, F, GH); 1 km N of hwy. Mex. 70, on gravel road N towards Est. Méndez, 6.2 km W of Canoas junction and 12 km NNW of Pánuco, Mun. Pánuco, 22°10'N, 98°12'W, 50 m, 24 Oct 1981 (fl, fr), *Nee* 22328 (F); Río Escondido, Mun. de Puente Nacional, 100 m, 24 Jan 1981 (fl), *Ventura 18132* (F). **Yucatán:** At Izamal, (fl, fr), *Gaumer 708* (A, BM, F); Chichankanal (fl), *Gaumer 1517* (F Chichen Itzá, near Castillo, Jun-Jul 1938 (fl), *Lundell & Lundell 7404* (A, F); Ruins of Uxmal, 16 Sep 1865 (fl, fr), *Schatt 657* (BM).

NICARAGUA**. Carazo:** Vicinity of Jinotepe, about 600 m, 20 May 1947 (fr), *Standley 8455* (F). **Chontales:** ca. 2.8 km above (N of) Cuapa, ca. 12°17'N, 85°23'W, 400-500 m, 4 Sep 1977 (fl, fr), *Stevens 3674* (BM). **Estelí:** Vicinity of Estelí, about 680 m, 1-3 Jun 1949 (fl), *Standley 20252* (F). **Granada:** East side, near summit above Finca Las Delicias, Volcan Mombacho, 8 Aug 1976 (fr), *Nelson 7597* (BM). **Jinotega:** Vicinity of Jinotega, 1030-1300 m, 19 Jun-9 Jul 1947 (fl), *Standley 9624* (F). **Madriz:** In mountains above Somoto, 800 m, 15 Nov 1946 (fr), *Williams & Molina 10939* (F, GH, US). **Matagalpa:** Ridge along road between La Danta and La Luna, ca. 12°40'N, 85°43'W, 960-1000 m, 30 Jul 1978 (fr), *Stevens 9607* (BM).

PANAMA**. Panama:** Barro Colorado Island, Lab clearing, by Kodak House, 21 May 1989 (fr), *Garwood 2985A* (BM, F), Near archeological site at edge of Madden Lake, 8 Apr 1972 (fl), *Gentry 5020* (F).

WEST INDIES. **Dominica:** St. Joseph Parish, En Haut Jean, near top of Haut Jean, 7 Dec 1964 (st), *Nicolson 2163* (MO, US); Au Vent, 10 m, 24 Apr 1946 (fr), *Stehlé 6401* (US); In silvis ad Laudad, 600 m, Feb 1882 (fl), *Toepffer 684* (BR, M); Northwest slopes of Morne Diablotins, Syndicate Estate, 600 m, 8 Oct 1983 (fr), *Whitefoord 3931* (BM); St. John, edge of Picard Gorge, south bank, 13 Apr 1992 (fl), *Whitefoord 7021* (BM, US).

Grenada: Opposite Woburn R.C. School, 10 Nov 1994 (fl, fr), *Barbour et al. 94119* (BM); Water Rock Reserve, Union, 12°36.152' N, 61°26.586'W, 390 ft, 1 Aug 2007 (fr), *Carrington & Sabir 2237* (US); Richmond Hill above Lowthers Lane, St. Georges, 24 Feb- 6 Mar 1950 (fl), *Howard 10683* (BM); La Borie, 4 Sep 1958 (fl), *Ramsammy 36* (US). **Guadeloupe:** Guadeloupe, Broussailles des environs du Camp Jacob, Feb 1894 (fr), *Duss 3408* (MO, US). **Martinique:** Martinique, 1909 (fl), *Duss 365* (M, US); Morne Cacao, Feb 1868 (fr) *Hahn 510* (BM, G, G, W); Morine du Vauclin (Sud), 400 m, 15 Feb 1939 (fl, fr), *Stehlé 3733* (US); Pitos de Canbet, 1000 m, 19 Dec 1942 (fl, fr), *Stehlé 6000* (US). **Mustique Island**: Jun 1890 (fl, fr), *Smith & Smith 976* (K). **Netherlands Antilles:** Windward Side Village, near Booby Hill, 17 Jan 1979 (fl, fr), *Fosberg 58986* (BM, US). **St. John:** Maho Bay Quarter, centerline road 4.5 km, 300 m, 19 Aug 1987 (fl), *Acevedo-Rodriguez et al. 1857* (US); Estate Bordeaux, Bordeaux Mt, east of peak, 350 m, 29 Jun 1985 (fl, fr), *Grifo & Matuszak 34* (MO); Mountains, 16 Aug 1949 (fr); *Vélez 3092* (K, US). **St. Lucia:** Marc district above Crown Lands, southwest of Piton Flore, 300-1000 ft., 4 Apr-12 Jun 1958 (fl, fr), *Proctor 17605* (BM, US). **St. Vincents:** Valley on the windward side, 1500 ft, May 1890 (fl, fr), *Smith & Smith 654* (K). **Tobago:** Mt. Dillon, 7 Dec 1949 (fl), *Baker & Dennis 14538* (K); Studley Park, 30 Jul 1909 (fl), *Broadway 3046* (G, MO); Great Dry River, Nov 1889 (fr), *Eggers 5749* (US); Ascent of Pigeon Hill, 18 Oct 1937 (fl), *Sandwith 1803* (K). **Tortola:** South side of Sage Mountain peak, 20 Apr 1965 (fl), *D'Arcy 86A* (MO). **Trinidad:** Chacachacare, 700 ft, 1 Apr 1951 (fr), *Baker 14691* (K); Gasparee Island, 2-7 Apr 1921 (fl), *Britton 2780* (K, US); Pointe Gourde, 31 Mar 1921 (fl, fr), *Britton & Broadway 2641* (US); Point Gourde, 28 Jul 1977 (fl), *Philcox 8081* (BM, K).

VENEZUELA. **Aragua:** Near Campanero, 1200 ft., 9 Mar 1857 (fl), *Fendler 2377* (GH); Rancho Grande, 3 May 1938 (fl), *Williams 10049* (F). **Bolivar:** E. of Miamo, Altipanicie Nuria, 300-500 m, 8 Jan 1961 (fr), *Steyermark 88174* (K, US). **Carabobo:** Between Las Trincheras and El Copey, main road Caracas-Co Guaira (fl), *Pittier 10255* (G, GH, NY, US); Lomas de Turiamo, 100-200 m, 5 Feb 1937 (fr), *Pittier 13868* (US). **Distrito Federal:** Between Caracas and La Guayra 16 Aug 1855 (fr), *Fendler 996* (GH, K); Cerro El Avila, a lo largo de la pica Hotel Humboldt-Papelón, 10°32.3' N, 66°52.4' W, 1990 m, 7 May 1992 (fl), *Meier 2136* (MO); Parque Nacional El Ávila, between Fila del Ávila and the city of Caracas, 1600-1900 m, 21 Jul 1979 (fr), *Nee & Whalen 16845* (F); Dept. Libertador, entre La Peñita y Chichiriviche, a lo largo del Río Chichiriviche, 12-14 km al sur de Chichiriviche, 10°31'N, 67°14'30"W, 500 m, 9 Oct 1976 (fl, fr), *Steyermark & Espinoza 112667* (US); Caracas, 1680 m, 1925 (fl), *Tate 33* (US). **Falcon:** Sierra de San Luis, cerca del Puente de Jobo, entre Curimagua y San Luis, 800-900 m, 20 Jul 1967 (fr), *Steyermark 99289* (US); Cerro Jacura, cumbre, 11°04'N, 68°51'W, 600 m, 3 Sep 1981 (fl, fr), *Sugden & Cardozo 743* (K). **Island of Margarita:** San Juan Mt., 790 m, 6 Jul 1903 (fr), *Johnston 69* (F, G, K, NY, US, W); El Valle to Juan Griego, 12-14 Aug 1903 (fl), *Johnston 350* (GH, US); **Island of Patos:** Patos, 9 Sep 1927 (fl), *Williams 11844* (K). **Merida:** Dist. Tovar, 5 km N of Zea, 8.25 N, 71.52 W, 2200 ft, 17 Oct 1978 (fl, fr), *Webster & Armbuster 23656* (MO). **Miranda:** Los Mariches, 22 Nov 1925 (fl, fr), *Pittier 11958* (A, G, US); **Monagas:** Cerro de la Cueva de Doña Anita, south of and bordering valley of Caripe, 1100-1200 m, 7 Apr 1945 (fl, fr), *Steyermark 61912* (F). **Táchira:** Entre San Juan de Colón (Dtto. Ayacucho) y la frontera con Colombia, aprox. 15 km en carretera montañosa arriba de San Pedro del Río, 1425 m, 19 Dec 1976 (fl), *Bunting & Chacón 4970* (K, NY); Entre Villa Páez y Tamá, arriba del Río Táchira, a lo

largo de la frontera Colombo-Venezolana, 2000-2200 m, 17-25 May 1967 (fl), *Steyermark & Dunsterville 98833* (US). **Yaracuy:** Entre el pueblo de Aroa y Altamira, 900 m, 22 Jan 1972 (fl), *Steyermark 105428* (US). **Zulia:** Vicinity of Perijá, 1918 (fl), *Tejera 191* (GH). **No State:** Vicinity of Cristobal Colon, 5 Jan -22 Feb 1923 (fr), *Broadway 221* (US).

Solanum leucopogon (8) Huber, Bol. Mus. Pará 4: 604. 1906. — TYPE: PERU. Canchahuaya, 26 Oct 1898, *J. Huber 1370* (lectotype, **here designated**: MG=F photo 1370!; isotype (fragment) F! [602866])

Solanum dimidiatum Sendtn., in Martius, Fl. Bras. 10: 102. 1846. non *S. dimidiatum* Raf (1840). — TYPE: BRAZIL. Rio Negro, Coari, *C. Martius s.n.* (lectotype, **here designated**: M! [M0147020] =F photo 6529!)

Woody vine to 10 m. Stems moderately armed with recurved, yellow to orange roselike prickles, these 2-5 mm long, the base 1.5-3 x 0.5-1 mm, moderately to densely pubescent with red, porrect-stellate hairs, the stalks nearly sessile to 0.5 mm, multiseriate, the rays 5-7, 0.5-1mm, unicellular to multicellular, the midpoints 1-5 (8) mm. Flowering portions of the stem consisting of difoliate sympodial units, the leaves usually geminate, those of a pair often slightly unequal. Leaves simple, the blades 8-20 x 2-15 cm, ovate, chartaceous, slightly discolorous, dark green-brown adaxially, light green-brown abaxially, with both leaf surfaces moderately to densely pubescent, the adaxial surface with hairs like those of the stem but the stalk absent, the abaxial surface with white hairs like those of the stem, major veins 4-7 on either side of the midvein, the midrib abaxially often with few recurved prickles like those of the stem; base obtuse, often asymmetrical; margin unlobed to 3-6 obtuse lobes per side, the sinuses cut less than ¼ to 1/3 of the way to the midvein; apex acute; petioles 0.5-4 cm, moderately pubescent with hairs like those

of the stem, sparsely to moderately armed with prickles like those of the stem, these often 2-ranked. Inflorescences 3-7 cm, extra-axillary, unbranched with 5-15 flowers, the plants andromonoecious, with male flowers on young plants and hermaphroditic flowers on older plants, the axes moderately to densely pubescent with hairs like those of stem, generally unarmed; peduncle absent to 2 cm; rachis 1-6 cm; pedicels 5-15 mm in flower, 10-20 mm in fruit; nearly contiguous, spaced 2-4 mm apart. Calyx 5-10 mm long, the tube 5-7 mm, the lobes 1-3 x 0.5-1 mm, triangular with acute to obtuse apices, often strongly recurved, moderately to densely pubescent with hairs like those of the stem, often with straight prickles 1-2 mm long; fruiting calyx 8-12 mm, not accrescent in fruit. Corolla 1-2.5 cm in diameter, charteacous, white, stellate, lobed nearly to the base, the lobes 5-10 x 2-4 mm, narrowly triangular, moderately to densely pubescent abaxially with white to red stellate hairs like those of the stem, sparsely pubescent adaxially. Stamens 4-8 mm; filaments to 1 mm, glabrous; anthers 4-8 x 1-2.5 mm, attenuate, tapering connivent, yellow, the base cordate, the apex obtuse, the pores apical, directed slightly introsely. Ovary sparsely pubescent with multicellular, uniseriate glandular hairs 0.2-0.4 mm long; style in functionally male flowers 2-3 x 0.5-1.5 mm, style in hermaphroditic flowers 7-10 x 0.5-1.5 mm, exserted beyond stamens, cylindrical, white, sparsely pubescent with glandular hairs like those of the ovary; stigma to 1 mm wide, cylindrical, green. Fruit a leathery berry, 1.5-2.5 cm in diameter, globose, green when immature, orange to red when mature, glabrous. Seeds 30-60 per fruit, reniform, brown, 2-2.5 x 1.5-2 mm, flattened, the surface netlike with many pits separated by small raised ridges (Fig. 4.18).

Habitat and distribution. (Fig. 4.13) In disturbed habitats including roadsides, forest gaps, and river sides in the eastern Andean foothills and adjacent lowlands from

northern Ecuador through Peru to Cochabamba Department, Bolivia with some collections from the Amazon Basin in Peru and Ecuador at 200-2500 m.

Etymology. Huber chose the epithet "leucopogon" from the Greek "leuco-" meaning "white" and "-pogon" meaning beard in reference to the dense white pubescence found on the flower buds.

Notes. *Solanum leucopogon* is most commonly collected in the eastern Andean foothills and adjacent lowlands from northern Ecuador through Peru. The cauline hairs of *S. leucopogon* make it among the most recognizable species in sect. *Eriophyllum*. The stems are typically densely pubescent with red, stellate hairs that have a short stalk (nearly sessile to 0.5 mm in length) but a greatly elongated midpoint (1-5 (8) mm in length). This species is sympatric through much of its range with *S. pedemontanum*; however, the latter species does not have the conspicuous cauline hairs and is recognizable by a dense white tomentum, especially on the abaxial leaf surfaces.

Solanum monachophyllum is weakly supported (67% BS, 1.0 PP) as the sister species of *S. leucopogon* (Stern and Bohs in prep). The range of these species possibly overlaps as both occur sporadically in the Amazon Basin; however, most collections of *S. leucopogon* are from the eastern foothills of the Andes while *S. monachophyllum* is more commonly collected in the Guiana Shield. Both species occur in disturbed habitats, however, *S. monachophyllum* is nearly exclusively found on river banks while *S. leucopogon* is common in light gaps in forests and roadside habitats. Morphologically *S. monachophyllum* is has nearly glabrous stems, small fruits, and much thinner corolla lobes and longer, narrower anthers than *S. leucopogon.*

The description of *S. leucopogon* in the "Boletim do Museu Goeldi (Museu Paraense)" does not specify the type locality. The collection at F has sparse material and

is likely a fragment of the MG specimen; therefore, we have designated the MG specimen to be the lectotype. The name *S. dimidiatum* was used by Rafinesque (1840) for a North American species of spiny solanum making the Sendtner name illegitimate. The only known specimen from the Sendtner name is at M where many of the collections used by Martius in "Flora Brasiliensis" are located, making this sheet the clear choice for lectotypification.

Additional specimens examined. BOLIVIA**. Cochabamba:** Prov. Chapare, on new road to Todos Santos, 135 km northeast of Chochabamba, north side of Rio San Mateo, near Chimore, 600 m, 9 Mar 1939 (fl), *Eyerdam 24715* (F, K) **Pando:** Mapiri Region, San Carlos, 850 m, 9 Jan 1927 (fl, fr), *Buchtien 1255* (US).

BRAZIL. **Acre:** North bank of Rio Juruá, opposite Cruzeiro do Sulm, 27 Oct 1966 (fl), *Prance et al. 2909* (US). **Amazonas:** Basin of Rio Jurua, Independencia, 26 May 1933 (fr), *Krukoff 4587* (A, G, GH, K, US); Mun. Humayta, near Tres Casas, 14 Sep- 11 Oct 1934 (fl), *Krukoff 6349* (K); Rio Purus between Lago Quati and Lago Arimã, near Rio Jacaré, 20 Jun 1971 (fr), *Prance et al. 13437* (GH, K, M, US); Rio Purus between Santa Maria and Mari N of Lábrea, 22 Jun 1971 (fr) *Prance et al. 13449* (US); Rio Juruá, Nov 1900 (fl), *Ule 5197* (G, K). **Rondônia:** 15.5 km E of Campo Novo on road to Ariquemes, Mun. Porto Velho, 10°35'S, 63°30'W, 300 m, 25 Apr 1987 (fr), *Nee 35038* (GH); Mun. Porto Velho, 6.5 km SW of Campo Novo, along Rio Brazo, 10°37'S, 63°38'W, 300 m, 26 Apr 1987 (fr), *Nee 35042* (F, K, US); Island in Rio Madeira opposite Rio Jaciparaná, 28 Jun 1968 (fr), *Prance et al. 5286a* (K).

COLOMBIA. **Amazonas:** Leticia, Quebrada de Arara, 360 m, 27 Jan 1969 (fr), *Cuatrecasas et al. 27262* (US). **Cauca:** Road Timbío-Veinte de Julio, near Veinte de Julio, 2000 m, 15 Oct 1974 (fr), *Maas & Plowman 2154* (GH).

ECUADOR. **Carchi:** Mira Canton, norte del Carmen, camino a Chical, 00°17'N, 78°13'W, 2000-2200 m, 10 Feb 1992 (fl), *Palacios et al 9801* (MO). **Morona-Santiago:** Carretera Méndez-Morona, km 28, 02°50'S, 78°10'W, 700 m, 6 Jul 1990 (fl, fr), *Gudiño 461* (F, MO); Cordillera de Cutucú, western slopes, along a trail from Logroño to Yaupi, ca. 2°46'S, 78°06'W, 1200 m, Nov 1976 (fr), *Madison et al 3197* (MO); Along new road Mendez-Morona, 650 m, 17 Aug 1989 (fl), *van der Werff & Gudiño 11185* (MO). **Napo:** Yasuni Forest Reserve, 1-3 km E of Pontificia Universidad Católica del Ecuador Scientific Station by Tiputini River, 0°40.853'S, 76°23.697'W, 240 m, 16 Jun 1995 (fr), *Acevedo-Rdgz. & Cedeño 7362* (F, US); Archidona Cantón, Parque Nacional Napo-Galeras, cima de la Cordillera de Galeras, 1700-1750 m, 26 Mar 1997 (fr), *Alvarez 1848* (MO); Orellana, Parque Nacional Yasuni, carretera y oleoducto de Maxus en construcción km 32, al sur del Río Tiputini, 0°37'S, 76°29'W, 250 m, 8-10 Feb 1994 (fl), *Aulestia 1687* (MO); Lake Lago Agrio, 0°07'N, 76°55'W, 250 m, 31 Mar 1980 (fl), *Brandbyge & Asanza 30376* (MO); Reserva Biológica Jatun Sacha, Río Napo, 8 km al E de Misahualli, 1°04'S, 77°36'W, 450 m, 21-25 May 1987 (fr), *Cerón 1448* (MO); Along road toward Parque Nacional Sumaco Napo Galleras, departing main Baeza-Agrio Hwy., 25.3 km S of Baeza turnoff, sector Gonzales Diaz de Pineda, 0.6 km before reaching village of Gonzalo Diaz de Pineda, 00°17'49" S, 77°45'12" W, 1469 m, 18 Aug 2004 (fl), *Croat et al. 93511* (US); Loreto, comunidad 10 de Agosto, Río Pucuno, bloque 19, línea sísmica 22, compañia Triton, 00°44'S, 77°32'W, 1000 m, 28 Mar 1996 (fr), *Freire & Cerda 288* (MO); Road to Bermejo oil field, 35 km N of "km 46" of Lago Agrio-Quito road, ridgetop, 10 km W of Lumbaque, 0°10'N, 77°20'W, ca. 950 m, 21 Jul 1986 (fl), *Gentry & Miller 54975* (MO); 3 km este del Caserío de Huamaní, al norte de la carretera Hollín-Loreto, 0°43'S, 77°36'W, 1200 m, 17 Sep 1988 (fr), *Hurtado & Alvarado 245*

(F); Carretera Hollín-Loreto, km 40, 5 km al oeste del Caserio de Huamani, faldas del volcan Sumaco, 00°43'S, 77°36'W, 1200 m, 7 Sep 1988 (fl), *Hurtado, Neill, & Alvarado 210* (F, MO); Cosanga, Carretera Cosanga El Aliso, a 1 km del partidero hacia El Aliso, 2240 m, 20 Aug 1990 (fl), *Jaramillo, Grijaiva, & Grijaiva 12009* (MO); Cascada San Rafaél (Coca Falls), turnoff (INECEL Campamiento Quipos, Proyecto Coca), 71.3 km NE of Baeza on Baeza-Lago Agrio (Neuvo Loja) road, 0°10'S, 77°40'W, 1200-1400 m, 25 Jan 1984 (fl), *Knapp & Mallet 6202* (US); Cañon de los Monos, road Coca (Puerto Francisco de Orellana) Lago Agrio, ca. 12 km north of Coca, 24 Jan 1973 (fl), *Lugo 2993* (K); San Pablo at Río Napo, 6-7 km south west of Coca (Puerto Francisco de Orellana), 28 Jan 1973 (fl), *Lugo 3062* (K, MO); Domingo Puerto at Río Napo, ca 10 km south west of Coca (Puerto Francisco de Orellana), 30 Jan 1973 (fl), *Lugo 3067* (K, MO); Archidona Canton**,** southern slopes of Volcán Sumaco, along Hollin-Loreto road, 0°35'S, 77°40'W, 1200 m, 26 Jan 1991 (fl), *Moran & Rohrbach 5184* (MO); Prov. Napo, Estación Biológica Jatun Sacha, Río Napo, 8 km al E de Misahualli. 1°04'S, 77°36'W, 450 m, 9 Jul 1988 (fr), *Neill et al 8498* (MO); 3 km de entrada a Estación Biológica Jatun Sacha, en camino a Río Arajuno, 01°04'S 77°37'W, 450 m, 30 Aug 1988 (fr), *Palacios 2810* (MO); El Chaco Canton, Sitio Tres Cruces, hacia El Mirador, 0°11'S, 77°42'W, 2000 m, 23 Jan 1991 (fl), *Palacios 6894* (MO); Quijos Canton, Cosanga, entre Río Vinillo y Río Cosanga, 00°34'S, 77°52'W, 2000 m, 13 Jan 1992 (fr), *Palacios, Rubio, & Alvarez 9622* (MO); Orellana, Yasuni National Park, Maxus road and pipeline construction project, km 10, banks of Rio Palometa, 0°29'S, 76°34'W, 250 m, 28 Jun 1994 (fr), *Pitman 443* (MO); Canton Quijos, 28 miles east of Baeza, before Salado, 5300 ft, 29 Jul 1974 (fl), *Plowman et al. 3939* (F, GH, K, US); Estación Científica Yasuní, Río Tiputini, al noroeste de la confluencia con el R. Tivacuno, este de la carretera Maxus, km 44, desvio hacia el pozo

Tivacuno, 00°38’S, 76°30’W, 200-300 m, 9 Jun 1995 (fl), *Romoleroux & Foster 1670* (F); Vicinity of Puyo, Prov. Napo-Pastaza, eastern foothills of the Andes, 750-1000 m, Aug 1939 (fl), *Skutch 4395* (A, GH, K, US); Quijos, Reserva Ecológica Antisana, Cordillera de los Guacamayos, entre Oleoducto secundario, compañia Arco, 00°39’S, 77°50’W, 1775 m, 14 Dec 1999 (fr), *Vargas & Narváez 3258* (MO). **Pastaza:** Via Anzu, N of Mera, 1°20’S, 78°10’W, 1100 m, 19 Mar 1988 (fl, fr), *Boom & Beardsley s.n.* (US); 31 km N of Puyo on road to Tena, side road E of Cajabamba, 1°15’S, 77°50’W, 1000 m, 25 Dec 1987 (fr), *Boom et al. 7795* (US); On north side of el Puyo, 29 Sep 1974 (fr), *Hudson 837* (MO); Lorocachi, sur oeste a del campamento militar, 1°38’S, 75°59’W, 200 m, 26 May 1980 (fl), *Jaramillo et al 31158* (K, MO); In vicinity of Colonia Játiva, ca 15 km north of Mera, 4 Jul 1968 (fl), *Lugo 105* (MO); Colonia 24 de Mayo, side road to road Puyo-Puerto Napo, ca 18-20 km from Puyo, 12 Sep 1968 (fl), *Lugo 393* (K, MO); Canelos, 6 Nov 1974 (fl), *Lugo 4460* (K, MO); 5 km al NE de Mera Carretera al Río Ansu, 01°26’S, 78°06’W, 1200 m, 3 Mar 1985 (fl), *Neill et al 5934* (MO); Pastaza, Colonia La Independencia, 30 km east of Puyo, proposed ARCO petroleum facility, 01°22’S, 77°45’W, 1000 m, 6 Sep 1997 (fr), *Neill et al 10913* (MO); Montalvo, on the Río Bobonaza, along the trail to Chiriboga, 2°05’S, 76°58’W, 300-350 m, 28 Jul 1980 (fl), *Øllgaard et al. 35500* (F, K); Pastaza Canton, Pozp Moretecocha, el sitio de plataforma, 01°04’S, 77°25’W, 580 m, 23 Aug 1992 (fl), *Palacios 10387* (MO); Via Auca, 115 km al sur de Coca, cerca del Rio Tigüino, carretera de PETRO-CANADA en construccion, 1°15’S, 76°55’W, 320 m, 24 May 1989 (fl, fr), *Rubio 159* (G); Pozo petrolero “Golondrina” de PETRO-CANADA, 25 km (aprox.) al NW del pueblo de Curaray, 01°10’S, 77°06’W, 400 m, 23 Jun 1989 (fr), *Rubio & Gudiño 182* (F, MO); Carretera de PETRO-CANADA en construcción, Via Auca, 115 km al sur de Coca, 6 km

al sur del Río Tigüino, 1°15'S, 76°55'W, 320 m (fr), *Zak & Rubio 4337* (MO). **Santiago-Zamora:** along Río Valladolid, around Tambo Valladolid, 2000 m, 14 Oct 1943 (fl), *Steyermark 54660* (W). **Sucumbios:** Río Bermejo to Cerro Sur Pax, Cofan community of Alto Bermejo, access from Bermejo oil field road to Pozo 2, NW between Lumbaqui and Cascales, vicinity of Vista Camp, 00°18'13.8 N, 77°24'32.0 W, 1200 m, 27 Jul 2001 (fl), *Aguinda, Pitman, & Foster 1029* (F); Gonzalo Pizarro, Reserva Ecológica Cayambe-Coca, parte baja del sendero a El Reventador, 00°06'S, 77°36'W, 1530 m, 12 Aug 1999 (fr), *Vargas et al 3985* (MO). **Tungurahua:** Valley of Pastaza River, between Baños and Cashurco, 8 hours east of Baños, 1300-1800 m, 25 Sep 1923 (fl), *Hitchcock 21857* (GH, US). **Zamora-Chinchipe:** Zamora Cantón, Romerillos Bajo, eastern border of Podocarpus National Park, quebrada Neya, Fundacion Maquipucuna: Bosque (plot) #2, 04°11'S, 78°55'W, 1550 m, 6 Nov 1996 (fl), *Clark et al 3301* (MO); Reserva San Francisco, km 30 along road Loja-Zamora, 03°59'S, 79°05'W, 2000 m, 21 Nov 1992 (fr), *Van der Werff et al. 19592* (BM). **No Dept:** Cerro Antisana, 3 miles S.W. of Tena, 0°30' S, 78°W, 2000 ft, 27 Aug 1960 (fl), *Grubb et al. 1454* (K).

PERU. **Amazonas:** Above Quebrada Huampami, 800-900 ft, 21 Nov 1972 (fr), *Berlin 324* (MO); Quebrada Huampami, monte, 600 ft, 17 Jul 1974 (fl), *Kayap 1183* (MO); Al lado Huampami, monte, 800-850 ft, 2 Aug 1974 (fl), *Kayap 1438* (MO); Al lado Huampami, monte, 800-850 ft, 3 Aug 1974 (fr), *Kayap 1475* (MO); Río Cenepa, vicinity of Huampami, ca. 5 km, E. of Chávez Valdívia, ca 4°30'S, 78°30'W, 200-250 m, 3 Aug 1978 (fl), *Kujikat 151* (MO) **Cajamarca:** Prov. San Ignacio, Huarango, Nuevo-Mundo, Pisaguas, 5°10'00"S, 68°32'00"W, 1550 m, 13 Nov 1997 (fr), *Campos & Nuñez 4627* (F, MO); Prov. San Ignacio, Huarango, localidad de Pisaguas, 5°14'52"S, 78°38'3"W, 1650 m, 11 Mar 2000 (fl, fr), *Campos et al 6568* (MO); Prov. San Ignacio,

Huarango, Nuevo Mundo, Caserío Gosén, 1500-1600 m, 21 Jul 1997 (fl ,fr), *Rodríguez & Reyes 1762* (MO). **Huánuco:** Prov. Pachitea, 20 Nov 1974 (fl), *Encarnación E-729* (MO); Prov. Pachitea, Dtto. Honoria, Bosque Nacional de Iparia, a lo largo del Río Pachitea cerca del campamento Miel de Abeja (1 km arriba del pueblo de Tournavista o unos 20 km arriba de la confluencia con el Rio Ucayali), en bosque bajo en el camino a Ayamiria, 300-400 m, 28 Nov 1966 (fl), *Schunke 1293* (F, G); Prov. Pachitea, Dtto. Honoria, Bosque Nacional de Iparia, a lo largo del Río Pachitea cerca del campamento Miel de Abeja (1 km arriba del pueblo de Tournavista o inos 20 km arriba de la confluencia con el Rio Ucayali), 17 Apr 1967 (fl), *Schunke 1859* (F); Prov. Pachitea, Dtto. Honoria, Bosque Nacional de Iparia, a lo largo del Río Pachitea cerca del campamento Miel de Abeja (1 km arriba del pueblo de Tournavista o inos 20 km arriba de la confluencia con el Rio Ucayali), 300-400 m, 16 Oct 1967 (fr), *Schunke 2232* (F, US); Prov. Leoncio Prado, road between Tingo Maria and Pucallpa, km 35, 9°10'S, 75°48'W, 1500 m, 3 Jun 1981 (fl), *Sullivan & Young 1145* (MO). **Junín:** Pichis Trail, Dos de Mayo, 1700-1900 m, 2-3 Jul 1929 (fr), *Killip & Smith 25863* (US). **Loreto**: Loreto Province, Campamento Forestal, 16 km from the Ecuador border near Río Conventes, 12 Apr 1979 (fr), *Aronson & Rodriges 854* (MO); Loreto, Andoas, 100 m, 23 Oct 1979 (fr), *Ayala 2198* (F, MO); Loreto, Tigre, Río Corriente, Teniente López, caserío Jíbaros, 26 Nov 1979 (fl, fr), *Ayala et al 2426* (MO); Prov. Maynas, Río Blanco a 3 horas desde Tamshiyacu (Johnson 40 hp), ca 130 m, 15 Mar 1978 (fl), *Díaz et al 179* (MO); Prov. Maynas, trocha detrás del Caserío de Huanta, ca. 130 m, 1 Sep 1979 (fl, fr), *Díaz et al 527* (F, G, MO); Prov. Coronel Portillo, Bosque Nacional Von Humboldt, borde de la carretera hacia los campamentos, km 89, Pucallpa-Tingo Maria road, 8°45'S, 75°05'W, 350 m, 3 Dec 1978 (fr), *Diaz et al 709* (F, MO); umgebung von Iquitos, 3°34'S, 73°W,

ca. 100 m, 23 Feb 1969 (fl, fr), *Doppelbaur 6-88/225* (M); Prov. Requena, Restinga Iricahua, abajo de S. Herrera margen izquierda del R. Veayal, 17 Feb 1982 (fl, fr), *Encarnación 1288* (MO); Prov. Alto Amazonas, Andoas, Río Pastaza near Ecuador border, 230 m, 16 Nov 1979 (fr), *Gentry & Díaz 28131* (MO); Prov. Maynas, short cut from Río Amazonas below Iquitos to Río Yanayacu, 120 m, 22 May 1978 (fr), *Gentry et al 22151* (MO); Iquitos, ca. 100 m, 3-11 Aug 1929 (st), *Killip & Smith 27408* (US); Iquitos Region, Padre Isla, 4 Jul 1966 (fl), *Martin & Lau-Cam 1082* (GH); Loreto Río Macusari below Ecuadorian border, 16 Sep 1968 (fl), *McDaniel & Marcos 10988* (F, MO); Above Pongo de Manseriche, first island in Rio Santiago, 200 m, 23 Dec 1931 (fl), *Mexia 6335* (G, GH, K); Prov. Maynas, Amazon Lodge, Río Yanayacu, 100 m, 19 Aug 1981 (fr), *Murphy & Díaz 123* (MO); Maynas Province, Iquitos, Padre Isla, 3 km al NW de Iquitos, Várzea, 3°45'S, 76°10'W, 100 m, 22 Sep 1990 (fl), *Pipoly et al 12300* (MO); Prov. Maynas, Río Ampiyacu, Pebas and vicinity, approx. 3°10'S, 71°49'W, 7 May 1977 (fr), *Plowman et al. 7306* (GH, MO); vicinity of Iquitos, ca. 120 m, 1977 (fl), *Revilla 3732* (MO); Prov. Maynas, Dtto. Iquitos, Isla Iquitos, Santa Martha, 14 Feb 1974 (fr), *Rimachi 856* (US); Prov. Maynas, Dtto. Punchana, Río Nanay, trocha de la Cocha de Manga Posa, frente al Puerto de Picuruyacu, ca. 90 m, 20 Jul 1994 (st), *Rimachi 11018* (US); Prov. Maynas, Dtto. Iquitos Carretera Iquitos-Nauta, km 21, trocha de pentración al caserio Yarana, Río Nanay, ca 120-150 m, 1 Aug 1996 (fl), *Rimachi 11778* (MO); Prov. Maynas, Varadero, Río Amazonas, camino a Mazan (Río Napo) 3°30'S, 73°10'W, ca. 115 m, 13 Nov 1980 (fl), *Vásquez 749* (MO); Prov. Maynas, Fatima, 45 minutes en dislizador hacia el norte de Iquitos, 3°40'S 72°55'W, 118 m, 12 Aug 1980 (fl, fr), *Vásquez et al 434* (K, MO, US); Prov. Maynas, Habanillo, km 67 carretera Iquitos-Nauta, 4°30'S, 73°30'W, 130 m, 8 Nov 1988 (fr), *Vásquez et al 11199* (GH, MO); Prov.

Maynas, Iquitos, Allpahuayo, estación experimental del Instituto de Investigaciones de la Amazonía Peruana (IIAP), 30 May 1990 (fr), *Vásquez et al 13793* (MO); Prov. Maynas, Progreso (Isla Iquitos), 3°50'S, 73°20'W, 106 m, 6 Apr 1985 (fr), *Vasquez & Jaramillo 6282* (MO); Prov. Requena, Sapuena, Bagazán-Río Ucayali, 4°45'S, 73°38'W, 130 m, 13 Jan 1987 (fl, fr), *Vásquez & Jaramillo 8749* (MO); Prov. Maynas, Indiana, Explorama Reserve, 3°28'S, 72°50'W, 106 m, 3 Oct 1989 (fr), *Vásquez & Jaramillo 12819* (MO); Prov. Maynas, Iquitos, Allpahuayo, estación experimental del Instituto de Investigaciones de la Amazonía Peruana (IIAP), 4°10'S, 73°30'W, 150-180 m, 23 May 1991 (fr), *Vásquez & Jaramillo 16380* (MO); Lower Río Nanay, May-Jun 1929 (fl), *Williams 517* (F); Manfinfa on the Upper Río Nanay, Jun-Jul 1929 (fl, fr), *Williams 1093* (F);La Vitoria on the Amazon River, Aug-Sep 1929 (fl), *Williams 2652* (F); Leticia on the Amazon River, Sep 1929 (fr), *Williams 3148* (F); Iquitos, 120 m, Mar-Apr 1930, (fr), *Williams 8054* (F). **Madre de Dios:** Tambopata, ca. 35 air km or 70-80 river km SSW Puerto Maldonado at effluence Rio La Torre (Rio D'Orbigny)/ Rio Tambopata (SE bank), Tambopata Nature Reserve, 12°49'S, 69°17'W, ca. 260 m, 28 Apr 1980 (fr), *Barbour 5022* (MO); Prov. Manu, Parque Nacional Manu, Río Manu, above Río Sotileja, 11°38'S, 71°54'W, 400-450 m, 12 Oct 1986 (fr), *Foster, d'Achille, & Cruz 11790* (F); Tambopata, alrededores del Albergue turistico Cusco Amazónico, margen izquierdo del Río Madre de Dios, ca. 35 km de Puerto Maldonado, 200 m, 29 Oct 1988 (fr), *Núñez et al 9982* (MO); Tambopata Province, Las Piedras, Cusco Amazónico, 12°29'S, 69°03'W, 200 m, 18 Oct 1991 (fr), *Timana & Jaramillo 2687* (MO). **Pasco:** Oxapampa, Pichis valley, San Matias ridge, 10-12 km SW of Puerto Bermúdez, above Santa Rosa de Chivis, trail to Loma Linda, 10°20'S, 75°00'W, 1000 m, 29 Sep 1982 (fr), *Foster et al 8971* (MO) **San Martín:** Prov. Mariscal Caceres, Dtto. Uchiza, 500 m, 23 Jun 1969 (fl),

Schunke 3208 (F, G, US); Prov. Mariscal Caceres, Dist. de Tocache Nuevo, camino al caserío de Almendras, 400 m, 7 Aug 1969 (fl), *Schunke 3308* (F, US); Prov. Mariscal Caceres, Dist. de Tocache Nuevo, carretera a Cachiyacu, 5 km de Puerto Pizana, 4 Oct 1971 (fr), *Schunke 5025* (F, G, GH, US); North of Uchiza, 450 m, 18 Jan 1962 (fl), *Vigo 5741* (F, MO); Prov. Mariscal Caceres, Dist. de Tocache Nuevo, vicinity of Tocache, 400-700 m, 1979 (fl), *Vigo 11046* (MO); Huinguillo, 500-600 m, 26 Mar 1962 (fl), *Woytkowski 7185* (US). **Santiago-Zamora:** Taisha, 1500 ft, 26 Jan 1962 (fl), *Cazalet & Pennington 7524* (K, US) **Ucayali:** Coronel Portillo, Campo Verde km 52 C.F. Bascoche, 250-270 m, 8 Feb 1989 (st) *Chavez 220* (MO).

Solanum monachophyllum (9) Dunal, Solan. Syn. 33. 1816. —TYPE: VENEZUELA. Río Orinoco, *A. Humboldt & A. Bonpland s.n.* (Holotype: P-HBK!; isotype B! [W04412-010]).

Solanum molle Dunal, Solan. Syn. 28. 1816. — TYPE: VENEZUELA. in Caracas, Río Guárico, *A. Humboldt & A. Bonpland* (Holotype P-HBK!; isotype B, photo of holotype (Morton neg. 8250: F!))

Solanum angustiflorum Mart. ex Sendtn., in Martius, Fl. Bras 10: 107. 1846. — TYPE: BRAZIL. Est. Bahia, Rio São Francisco, at Joazeiro, Apr, *C. Martius s.n.* [*2394*] (Holotype: M! [M-0147019], =F photo 6524!).

Solanum sacupanense Rusby Descr. New Sp. S. Amer. Pl. 115. 1920. — TYPE: VENEZUELA. Lower Orinoco, Sacupana, Apr 1896 (fl, fr), *Rusby & Squires 22* (lectotype: NY! [00172161], (designated by Dorr, 1995); isolectotypes: BM! [BM000514919], G! [G00227717], NY! [00172162], US! [00731250], US! [00731252], US! [00776821], US! [00027783], W! [5340]).

Names associated with this species that have not been validly published: *Solanum javitense* Kunth., Nov. Gen. & Sp. 3: 42. 1818. *Solanum cucuyense* Pittier, in H. Pittier et al., Cat. Flora Venez. 2: 370. 1947. *Solanum topirito* Pittier, in H. Pittier et al., Cat Fl. Venez. 2: 370. 1947.

Shrub to scandent shrub 1-2 m. Stems sparsely armed with recurved, yellow to brown roselike prickles, these 1-2.5 mm long, the base 1-2 x 0.5-1 mm, moderately pubescent with tan to rusty, porrect-stellate hairs, the stalks nearly absent to 1 mm, multiseriate, the rays 6-10, 0.5-1 mm, unicellular to multicellular, the midpoints reduced and appearing gland-tipped to 1 mm. Flowering portions of the stem consisting of difoliate sympodial units, the leaves usually geminate but occasionally spaced up to 2 cm apart, leaves of a pair slightly unequal. Leaves simple, the blades 2-11 x 1-5 cm, ovate, leaves chartaceous, slightly discolorous, dark green adaxially, green to whitish green abaxially, with both leaf surfaces moderately to densely pubescent with white hairs like those of the stem with midpoints often elongated to 1 mm; major veins 4-6 on either side of the midvein, the midrib unarmed; base acute; margin unlobed to 2-3 obtuse lobes per side, the sinuses cut less than ¼ of the way to the midvein; apex acute to obtuse; petioles 1-2 cm, moderately to densely pubescent with hairs like those of the stem, unarmed or occasionally with sparse prickles like those of the stem. Inflorescences 3-4 (7) cm, leaf-opposed to extra-axillary, unbranched, with 3-8 flowers, apparently all perfect, the axes glabrous to moderately pubescent with hairs like those of the stem, unarmed; peduncle 0.5-2 cm; rachis 1-3.5 (6) cm; pedicels 5-20 mm in flower and fruit, nearly contiguous, spaced 1-3 mm apart. Calyx 2-5 mm long, the tube 3-4 mm, the lobes 1-2 x 0.25-0.75 mm, triangular, moderately pubescent with hairs like those of the stem, unarmed; fruiting calyx 7-10 mm, lobes triangular, not accrescent in fruit. Corolla 1.5-2 cm in diameter,

chartaceous, white, stellate, lobed nearly to the base, the lobes 7-12 x 1-2.5 mm, narrowly triangular, moderately pubescent abaxially with hairs like those of the stem, glabrous adaxially. Stamens 6-8 mm; filaments 2-3 mm long, glabrous; anthers 4-6 x 0.5-1.5 mm, attenuate, tapering, connivent in bud, connivent to spreading in flower, yellow, the base cordate, the apex obtuse, the pores apical, directed slightly introrsely. Ovary glabrous to sparsely pubescent with glandular hairs; style 10-12 x 0.25-0.75 mm, occasionally reduced to 3-4 mm in length implying andromonoecy, exserted beyond stamens, cylindrical, white, glabrous; stigma to 1 mm wide, clavate. Fruit a berry, 8-12 mm in diameter, globose, green when immature, orange when mature, glabrous. Seeds 25-40 per fruit, reniform, brown, 1.5-2 x 1-1.5 mm, flattedned, the surface netlike with many pits separated by small raised ridges (Fig. 4.19).

Habitat and distribution. (Fig. 4.20) *Solanum monachophyllum* is found along riverbanks, often occurring on sandbars that may be up to 3 m below the high water mark of the Guiana Shield in Suriname, French Guiana, Guyana, and Venezuela and into the Amazon Basin on the Rio Negro and Amazon Rivers in Brazil at 20-250 (450) m.

Etymology. The epithet is from the Greek “monachos-” meaning “single or solitary” and “-phyll” meaning “leaf”.

Notes. *Solanum monachophyllum* is found at low elevations throughout northern South America from Bolivar Department, Colombia in the west to French Guiana in the east and Para, Brazil in the south. Nearly all collection labels indicate that the species occurs along or near rivers or streams. Field observations of *S. monachophyllum* on the Essequibo River in Guyana found the species growing on sandbars with what appeared to be a persistent woody base and annual growth of small, herbaceous shoots (Fig. 4.19).

These sandbars were above water in the dry season but the high water marks on the riverbanks indicated that they could be as much as 3 m underwater in the wet season.

Although there is variability between collections, *S. monachophyllum* is consistently the least prickly species of the section, perhaps due to the fact that it rarely climbs on other vegetation and thus does not require the roselike spines for climbing. The leaves of *S. monachophyllum* are widest below the midpoint and are typically unlobed but rapidly growing shoot might have 2-3 coarse lobes per side. The stamens of *S. monachophyllum* often appear to be disorganized, that is some stamens in a given flower might be slightly longer or spreading while others are more tightly connivent.

Phylogenetic results weakly support (67% BS, 1.0 PP) a sister relationship between *S. monachophyllum* and *S. leucopogon* (Stern and Bohs in prep). This relationship is unexpected as the species differ in habitat, geographic location, and multiple morphological characters. The low resolution of the backbone of the phylogeny and the unique morphological characteristics of *S. monachophyllum* make it difficult to definitively place within the section.

Solanum cucyense and *S. topirito* were both published without Latin diagnoses, making them invalid.

Additional specimens examined. BRAZIL. **Amazonas:** Sandy shore of the Rio Negro (fl, fr), *Deef 50* (K); Mun. de Novo Ayrao, Arquipélago de Anavilhanas (Rio Negro), 02°00’S, 60°27’W, 23 Jan 1992 (fr), *Ferreira 94* (K); Vicinity of Manaus, Tarumã Grande, 1 km N from the junction of Rio Negro and Igarape Tarumã, 3°2’S, 60°8’W, 9 Nov 1977 (fl), *Keel & Ramos 257* (K, MO, US); Manáos, 25 m, 13 Oct 1929 (fl ,fr), *Killip & Smith 30045* (US); Varzea along Rio Negro opposite Manaus, 30 Sep 1971 (fl, fr), *Maas & Maas 476* (K, MO); Río Apaporis, Soratama, 14 Feb 1952 (fl, fr),

Schultes & Cabrera (GH); Margin of Rio Negro, 25 Dec 1874 (fl, fr), *Traill 583* (K); Lower Amazons, beside the Jaucari, 22 Nov 1873 (fl), *Traill 584* (K); Riverside and small islets of Rio Negro within 100 km upper-stream from Manaus, 13 Aug 1987 (fr), *Tsugaru & Sano B-986* (A, MO); Manoias, Rio Negro, Mar 1901 (fl, fr), *Ule 5439* (G); Rio Branco, Jan 1909 (fl), *Ule 7830* (G, K, US). **Pará:** Municipio de Oriximina, Rio Trombetas, margem direita lago do Batata ao Norte de Porto Trombetas, 24 Jul 1980 (fl, fr), *Cid et al 1789* (K); Mun. do Oriximina, Cachoeira Porteira, 2 Jul 1980 (fr), *Davidson & Martinelli 10698* (US); Santarem, 12 Jan 1981 (fl, fr), *Krapovickas & Cristóbal 37133* (F, MO); Santarem, Muyaca (fl, fr), *Spruce 368* (K); In vicinibus Santarem, Nov-Mart. 1849-1850 (fl), *Spruce 496 "Solanum 4"* (BM, K, M, W). **Roraima:** Rio Univini entre Ponto 05A e a Boca, 25 Apr 1974 (fr), *Pires et al. 14283* (US); Rodovia BR-401, Boa Vista para Bom Fin, Río Arraia, perto de Guiana, 27 Jun 1974 (fl), *Pires & Leite 14712* (US); Boa Vista- Caracarai Road, (BR174), 58 km. S. of Boa Vista, 31 Jan 1969 (fl), *Prance et al. 9513* (K); Boa Vista, região do R. Cauaue, afluente do R. Branco, 12 Feb 1977 (fl, fr), *Rosa & Cordeiro 1470* (MO). **Unknown loc:** In insulis arenosis flum. Amazon, versus Sespa (or Serpa?) Mar 1832 (fl, fr), *sin col. s.n.* (W).

COLOMBIA. **Arauca:** Cravo Norte, campamento Sam., Arenales y playas del Río Casanare, Jul 1954 (fr), *Llano 33* (US). **Bolivar:** Municipio Achi, corregimiento La Raya, ciénaga La Raya en bosques alrededor de ciénaga grande, refugio "El Paraíso", 3-4 h de Caucasia, sobre el rio Cauca, 8°20'N, 74°30'W, 20-80 m, 5 Jul 1987 (fl), *Callejas et al 4339* (MO). **Boyacá:** Los Llanos, on Caño Guira, near mouth (Río Meta), 150 m, 22 Feb 1939 (fl), *Haught 2623* (K, US). **Santander:** Carare, Jul 1939 (fl, fr), *Bro. Daniel 2055* (F, US). **Vichada:** Parque Nacional Natural "El Tuparro", along border of Río Orinoco, ca. 1 km below mouth of Río Tuparro, 5°16'N, 67°52'W, ca. 80 m, 25 Feb 1985

(fl, fr), *Zarucchi & Barbosa 3408* (MO); Parque Nacional Natural "El Tuparro", ca. 6 km WSW of Centro Administrativo, south edge of Laguna Guaipé, 5°19'N, 67°53'W, ca. 80 m, 27 Feb 1985 (fl), *Zarucchi & Barbosa 3485* (MO); Parque Nacional Natural "El Tuparro", lower part of Cano Arepa, a tributary of the Rio Tomo ca. 16 km WSW of La Linea Roja, 5°26'N, 68°39'W, ca. 100 m, 14 Mar 1985 (fr), *Zarucchi & Barbosa 3704* (MO).

FRENCH GUIANA. **No Dept:** Amont de Touinké sur l'Itany (Haut Maroni), 25 Nov 1977 (fl, fr), *Cremers 5106* (MO); Camp 1 Ouman fou Langa Soula- Bassin du Haut-Marouini, 2°53'N, 54°00'W, 150 m, 24 Aug 1987 (fl, fr), *Granville et al. 9639* (US); Fleuve Maroni, entre Kaiapou et Papaichton, 28 Apr 1975 (fl), *Sastre & Moretti 4016* (MO).

GUYANA. **Cuyuni River:** Along river, Oct 1904 (fl, fr), *Bartlett 8253* (K); Cuyuni River, between Aurora and +/- 4 km upstream, 6°48' N, 59°46' W, 60 m, 8 Oct 1989 (fl, fr), *Gillespie & Tiwari 2187* (US). **Mazaruni River:** Sep 1880 (fl), *Jenman 778* (K). **Rupununi:** North Rupununi, Apr 1968 (fl, fr), *Davis 895* (K); Simony Creek, 100-250 m, 20 Nov 1992 (fl), *Görts-van Rijn et al. 344* (K); Dadanawa, Rupunini River, 2°50'N, 59°30'W, 100-150 m, 13 Jan 1991 (fl), *Jansen-Jacobs 2038* (MO); Kuyuwini Landing, Kuyuwini River, 2°05'N, 59°15'W, 200 m, 7 Feb 1991 (fl), *Jansen-Jacobs et al. 2436* (K, US); Kuyuwini Landing, Kuyuwini River, 2°05'N, 59°15'W, 150-250 m, 13 Oct 1992 (fl), *Jansen-Jacobs et al. 2902* (K, US). **Siparuni-Potaro:** Iwokrama Rainforest Reserve, between Pakutan Falls and Levi Falls on Siparuni River, 04°45' N, 59°01' W, 75 m, 10 Nov 1995 (fl), *Clarke 475* (US); Iwokrmama Rainforest Reserve, Essequibo River near Ladysmith Creek, 4°17'N, 58°30'W, 65 m, 20 Mar 1996 (fl), *Clarke 1385* (MO, US); Turtle Mountain, transect from Essequibo River to summit of Turtle

Mountain, 2.5 km W of Essequibo River, 04°43'N, 58°42'W, 200 m, 1 Oct 1996 (fl), *Clarke 2692* (US); Essequibo River at Karupukari crossing, beach on Indian House Island, 1 km N, 4°40'N, 58°41'W, 50 m, 18 Apr 1992 (fr), *Hoffman & Gharbarran 1294* (MO, US); Iwokrama, Siparuni River, Pakatau Falls and 2 km downstream, 4°44'N, 59°01'W, 100 m, 1 Dec 1994 (fr), *Mutchnick & Allicock 472* (K, MO, US); Iwokrama, Essequibo River, Kurupukari Falls, 4°40'N, 58°40'W, 100 mm 11 Dec 1994 (fl, fr), *Mutchnick & Funk 646* (US). **Upper Takutu-Upper Essequibo:** Maparri Creek, N side, opposite camp at base of waterfall, 03°20'N, 59°15'W, 4 Jun 1996 (fl), *Clarke & McPherson 1977* (US); Kamoa River, 0-6 km W of camp, 01°31'N, 58°49'W, 270 m, 9 Nov 1996 (fl, fr), *Clarke 3008* (US); Essequibo River between camp (at confluence of Essequibo River and Onoro Creek) and Konashen Rapids 01°35'N, 58°37'W, 240 m, 18 Nov 1996 (fl, fr), *Clarke 3278* (US); Rewa River, gorge below Great Falls, 3°10'N, 58°48'W, 90 m, 11 Feb 1997 (fr), *Clarke 3537* (K, US); Rema River, at confluense of Kwitaro River, 3°17'N, 58°45'W, 90 m, 25 Feb 1997 (fl), *Clarke 3868* (MO, US); Kuyuwini River watershed, Aishalton Landing, upstream 1 km S and N banks, 02°03'N, 59°09'W, 250 m, 21 Sep 1993 (fl, fr), *Henkel et al. 3092* (US); Acarai Mts, Watuwau Creek, 6-10 km upstream of juncture with Chodikar River, 1°22'N, 58°42'W, 250 m, 23 Feb 1994 (fr), *Henkel et al 4669* (BM, MO, US); Kassakaityu River, 25 km upstream for juncture with Essequibo River, 1°50'N, 58°45'W, 250 m, 24 Mar 1994 (fr), *Henkel et al 5334* (BM, MO, US); Takutu River near St. Ignatius Mission, 350 ft, 8 May 1937 (fl), *Mather s.n.* (US); Along high banks of Ireng River (border with Brazil) near crossing to Normandia, 3°53'N, 59°35'W, 100 m, 16 Feb 1990 (fl), *McDowell & Tiwari 1844* (US); Near Lake Surama and Surama village, 4°09'N, 59°09'W, 65 m, 22 Feb 1990 (fr), *McDowell 1990* (US); Between Onoro and Karinri, 24 Nov 1935 (fl), *Myers 5734* (K).

Puruni River: Mazaruni River, 16 Mar 1953 (fl, fr), *JB 37* (K). **Rupununi:** Lethem, east bank of Takutu River, 18 Apr 1956 (fl, fr), *Irwin 755* (US); same loc. (fr), *Irwin 786* (US). **No location:** Kamoa River, 01°32'N, 58°50'W, 260 m, 22 Sep 1989 (fl, fr), *Jansen-Jacobs et al. 1772* (K, US); Conservation International concession on the Essequibo River, 3°31'24.8"N, 58°15'2.1"W, 133 m, 28 Jan 2007 (fl, fr), *Redden et al. 5287* (US); sin loc (fl), *Schomburk 1135* (K); Basin of Essequibo River, near mouth of Onoro Creek, ca. 1°35'N, 15-24 Dec 1937 (fl), *Smith 2804* (US); Northwestern slopes of Kanuku Mountains, in drainage of Moku-moku Creek (Takutu tributary) 150-400 m (fl), *Smith 3521* (F, K, US).

SURINAME. **No Dept:** Bank of R. Tapanahony at level of Manlobi Mts., 31 Oct 1962 (fl), *Boer 236* (K); Prope stationem Victoriam in reg. inter. ad fl. Surinam, Dec 1843 (fl), *Kappler 1375* (G, G, MO, W); In montibus, qui dicuntur Nassau, along bank of river Marowijne, 14 Feb 1949 (fl, fr), *Lanjouw & Lindeman 2042* (K).

VENEZUELA. **Amazonas:** Orillas de los Ríos Manapiare y Ventuari, río abajo entre San Juan de Manapiare y la desembocadura del Manapiare en el Ventuari y río arriba en el Ventuari, entre la desembocadura del Manapiare y la desembocadura del Río Asita, 5°18'-5°04'N, 66°03'-65°50'W, 375-425 m, 29-31 Mar 1973 (fl, fr), *Agostini 1513* (F, K, MO); Orillas de los Ríos Manapiare y Ventuari, río abajo entre San Juan de Manapiare y la desembocadura del Manapiare en el Ventuari y río arriba en el Ventuari, entre la desembocadura del Manapiare y la desembocadura del Río Asita, 5°18'-5°04'N, 66°03'-65°50'W, 375-425 m , 29-31 Mar 1973 (fl, fr), *Agostini 1535* (F, MO, US); Dept. Atures, Río Sipapo, Pto Sipapo a 2 h de Pto Ayacucho, 6°34'N, 67°5'W, 25 Mar 1993 (fl, fr), *Castillo 3440* (MO); Dept. Atures, Río Sipapo, Pto Sipapo a 2 h de Pto Ayacucho, 6°34'N, 67°5'W, 25 Mar 1993 (fl, fr), *Castillo 3441* (MO); Municipio Autana, Ríos

Sipapo-Orinoco, margen derecha, 4°54'-5°3'N, 67°34'-67°46'W, 225 m, 15 Apr 1997 (fl), *Castillo 4798* (MO); Mun. Autana, Ríos Cuao-Sipapo, entre Piedra Chamii e Isla Lencho, 4°54'-5°3'N, 67°34'-67°46'W, 12 May 1998 (fl), *Castillo 5712* (MO); Unos 10 km inferiors al Río Ocamo, 14 May 1971 (fl), *Foldats 368-A* (US); Depto. Atabapo, caserio Macuruco, a orillas del río Orinoco, a unos 80 km al oeste de San Fernando de Atabapo, 3°57'N, 67°1'W, 99 m, 19 May 1981 (fl, fr), *Guanchez 1037* (MO); Dpto. Atabapo, ribera del río Orinoco, junto a caserío Macuruco, al este de San Fernando de Atabapo, 3°58'N, 67°6'W, 100 m, 19 Mar 1982 (fl, fr), *Guanchez 1518-A* (MO); Río Orinoco, ca. 100 m, 12-14 Jan 1930 (fr), *Holt & Gehriger 262* (US); Brazo Casiquiare, 1-20 Feb 1931 (fl, fr), *Holt & Blake 654* (F, US); Depto. Atures Santa Rosa de Ucata, approx. 4°24'N, 67°48'W, 80 m, 18 Apr 1989 (fl, fr), *Romero & Guanchez 1810* (MO); Depto. Río Negro, selvas pluviales en los alrededores de las orillas del río Casiguiare, entre Guachapita y El Porvenir, 15 Apr 1985 (fr), *Stergios et al 8106* (MO); Selvas pluviales cercanas y a las orillas del Rio Siapa, entre la Piedra del Cabezón y la Piedra de la Navtividad, approx 2°15'N, 66°25'W, 175 m, 16-27Jan 1987 (fl, fr), *Stergios et al 9864* (MO); Isla Caimán del Medio Ventuari, Mar 2002, (fl), *Stergios et al. 19845* (MO); Depts. Atures y Atabapo bosque ribereño parcialmente inundado de la ribera sur y norte del río Orinoco, poco más abajo de la confluencia con el río Ventuari, alrededores de Santa Barbara del Orinoco, 3°59'N, 67°03'W, 90 m, 12 May 1978 (fr), *Steyermark et al 117136* (MO, US); Depto. Aripao, Isla Ratón, Río Orinoco, 5°09'N, 67°45'W, 80 m, Oct 1989 (fl), *Velazco 603* (MO); Pto. Ayacucho, 100 m, 20 May 1940 (fr), *Williams 13039* (F, US); Pto. Ayacucho, 90 m, 27 May 1940 (fr), *Williams 13150* (F, US); En las abras alrededor de Pto. Ayacucho, 95 m, 27 May 1940 (fr), *Williams 13155* (A, F, US); El Cocuy, Río Negro, 100 m, 8 Mar 1942 (fr), *Williams 14713* (F, G); Esmeralda, Upper

Orinoco, 130 m, 1942 (fl, fr), *Williams 15509* (F); Puerto Ayacucho, about 100 m, May 1931 (fl), *Holt & Blake 783* (F, US); En los conucos de San Carlos de Río Negro, 100 m, 3 Mar 1942 (fl), *Williams 14689* (US); Sanariapo, Puerto Ayacucho, 120 m, 15 Apr 1942 (fl, fr), *Williams 14963* (F, US); Tamatama, Upper Orinoco, 130 m, 6 May 1942 (fr), *Williams 15200* (F, G, US). **Anzoategui:** Laguna y caño Mamo, 40 km al Oeste de San Félix, 30 May 1988 (fl), *Colonnello 1183* (MO); Municipio Independencia, Río Orinoco, margen izquierdo, La Ceiba, Frende a Ciudad Bolívar, 8°9'14.2"N, 63°32'50.5"W, 10-20 m, 13 Jul 2003 (fr), *Diaz et al 6349* (MO); Distrito Monagas, a 10 minutos de la población de Mapire, 7°30'-8°30'N, 64°30'-65°00'W, 50 m, 15 Feb 1995 (fl), *Flores et al 117* (MO); Along highway 13, 5 km SE of La Encrucijada, 57 km SE of Barcelona, 9°45'N, 64°30'W, 200 m, 27 Oct 1977 (fr), *Steyermark et al 115404* (MO). **Apure:** Dist. Muñoz, Hato "El Polvero", 79 km al S de Elorza, approx. 6°38'N, 69°37'W, 80 m, 28 Apr 1987 (fr), *Aymard et al 5667* (MO); Dist. Pedro Camejo, P.N. Santos Luzardo, Río Capanaparo, entre "La Macanilla" y "San Andres", 7°00'-7°03'N, 67°31'-67°37'W, 40 m, 18 May 1990 (fr), *Castillo et al 3171* (MO); Dist. Pedro Camejo, P.N. Satnos Luzardo, Río Capanaparo, Isla "Lindabarro", desembocadura del Capanaparo en el Orinoco, 7°03'-7°05'N, 67°04'-67°06'W, 32 m, 21 May 1990 (fl, fr), *Castillo et al 3229* (MO); Apure seco near San Fernando, 15 May 1940 (fl, fr), *Chardon 65* (US); Dist. San Fernando, Isla Arapuca in the Río Orinoco near the mouth of the Río Apure, 7°38'N, 66°25'W, 35 m, 25 Apr 1977 (fl), *Davidse & González 12111* (MO); Dist. San Fernando, between the bank of the Río Orinoco, opposite Isla Peladura, and the lagunas ca. 1 km inland, 7°15'N, 66°51'W, 35 m, 25-26 Apr 1977 (fr), *Davidse & González 12121A* (BM, MO); Dist. Pedro Camejo, 2.5 km upstream from the mouth of the Río Capanaparo at its junction with the Río Orinoco directly west of Isla La Urbana, 7°10'N, 67°3'W, 30 m, 5

May 1977 (fl, fr), *Davidse & González 12652* (MO); Dist. Pedro Camejo, banks of the Río Capanaparo between caños La Pica and La Guardia, 14 km directly (in a straight line) SW of Urañon, 6°54'N, 67°18'W, 35 m, 6-7 May 1977 (fl, fr), *Davidse & González 12793* (MO); Dist. Pedro Camejo, 11 km directly (in a straight line) E of Paso de San Pablo and ca. 2 km ENE of Fundo Picachón along the banks of the Río Capanaparo, 7°2'N, 67°39'W, 45 m, 8-9 May 1977 (fl, fr), *Davidse & González 12837* (MO); Dist. Pedro Camejo, 4 km directly (in a straight line) NE of El Btun along the banks of the Río Capanaparo, 6°58'N, 67°49'W, 55 m, 10-11 May 1977 (fl), *Davidse & González 13076* (MO); Dist. San Fernando, north bank of the Río Orinoco north of Isla Urbana and Isla Catarrosa, 7°12'N, 66°55'W, 40 m, 13 May 1977 (fl), *Davidse & González 13181* (MO); Dist. San Fernando, mouth of the Río Arauca at its intersection with the Río Orinoco, 7°24'N, 66°36'W, 35 m, 14-15 May 1977 (fl), *Davidse & González 13195* (MO); Dist. San Fernando, banks of the Río Arauca, 5 km directly (in a straight line) ESE of Güirimita, 7°22'N, 66°46'W, 35 m, 16-17 May 1977 (fl), *Davidse & González 13292* (MO); Dist. San Fernando, banks of the Río Arauca, 5 km directly (in a straight line) SW of El Faro, 7°19'N, 66°54'W, 35 m, 18-19 May 1977 (fl), *Davidse & González 13390* (MO); Dist. Pedro Camejo, banks of the Río Meta near the Brazo La Martinera, 19.5 airline km W of Mata de Guanábano, 6°11'N, 68°24'W, 65 m, 14 Feb 1978 (fl), *Davidse & González 14064* (MO); Dist. Pedro Camejo, along the Río Meta at the junction of the Caño Siriaco, 15.4 km airline km W of Buena Vista 6°10'N, 68°45'W, 70 m, 15 Feb 1978 (fl), *Davidse & González 14099* (MO); Dist. Muñoz, Caño Caicara, 11 airline km W of Mantecal gallery forest, 7°34'N, 69°15'W, 80 m, 3 Mar 1978 (fl, fr), *Davidse & González 14733* (MO); Dist. Rómulo Gallegos, north bank of the Río Capanaparo, ca. 33 airline km SW of Elorza, 6°48'N, 69°40'W, 85 m, 7 Mar 1979 (fl), *Davidse & González*

16143 (MO); Dist. Pedro Camejo, P.N. Santos Luzardo, Río Orinoco, sector "Los Caimanes", cerca de la desembocadura del Capanaparo, 7°05'-7°07'N, 67°03'-67°05'W, 32 m, 20 May 1990 (fl), *Duno et al 274* (MO); Dist. Pedro Camejo, P.N. Santos Luzardo, Río Orinoco, "Boca de Arauquita", desembocadura del Capanaparo, frente de la Urbana, 7°08'-7°10'N, 67°01'-67°04'W, 32 m, 20 May 1990 (fr), *Duno et al 320* (MO); Along long burrow pit to east of Módulo UNELLEZ, Lagune Hermosa Quadrangle #6238, 90 m, 22 Jan 1993 (fl, fr), *Phillippe et al 21421* (MO). **Barinas:** N side of Nutrias, 6 May 1971 (fl), *Nee & Mori 4166* (US); Reserva Forestal Ticoporo, Socopo, 10 Apr 1983 (fl), *Stergios et al. 5738* (MO); Reserva Forestal Ticoporo, Socopo, 10 Apr 1983 (fl, fr), *Stergios et al 5739* (MO); ½ km north of Barinitas, 800 m, 14 Apr 1968 (fl, fr), *Steyermark et al 102291* (MO). **Bolivar:** Ciudad Bolivar and vicinity, on the Orinoco, 200 ft, 6 Mar 1921 (fl, fr), *Bailey & Bailey 1805* (US); Dist. Cedeño, along road from the Caicara to Puerto Ayacucho, 12-72 km S of the junction with the road to Ciudad Bolivar, ca. 7°00'N, 66°30'W, 60-100 m, 26 Apr 1986 (fl, fr), *Boom 6579* (MO); Distrito Cedeño, valley of Caño Colorade, vicinity of Panare Indian village, ca 30 km SW of National Guard post at Maniapure, 6°45'N, 66°37'W, ca. 200 m, 5-7 Apr 1985 (fl, fr), *Boom & Eisenburg 6027* (K, MO, US); Ciudad Bolívar, 35 m, 16 Nov 1929 (fl), *Gehrigen 139* (G); Ciudad Bolívar, ca. 35 m, 4-25 Nov 1929 (fl), *Holt & Gehriger 139* (US); Ciudad Bolívar, ca. 35 m, 8-11 Jun 1931 (fl), *Holt & Blake 842* (US); Paso de Caruachi, lado N del Río Caroní, 75 km al E de Ciudad Bolivar, approx. 8°10'N, 62°50'W, 100 m, 31 Mar 1985 (fl, fr), *Holst et al 1959* (MO); Paso de Caruachi, lado S del Río Caroní, 75 kms al E de la Ciudad Bolivar, approx. 8°10'N, 62°50'W, 100 m, 6 Apr 1985 (fl, fr), *Holst et al 2270* (MO); Río Paragua, between La Paragua and Salto de Auraima, 260-270 m, 8 Apr 1943 (fl), *Killip 37275* (F, US); Boca Nichare, afluente izquierdo del Río Caura, 6°30'N,

64°50’W, 1994/1995 (fl, fr), *Knab-Vispo 340* (MO); San Pedro de las Dos Bocas, west bank of river, 6°59’N, 62°59’W, ca. 200 m, 24 Jul 1978 (fr), *Liesner & González 5525* (MO); Caño Pablo, tributario del Rio Caura 5-5, 5 km Sur Salto Para (Campamento las Pavas) 240 m, 7 May 1982 (fr), *Morillo & Liesner 8959* (K); Dist. Sucre, Orillas de la carretera Ciudad Bolívar-Maripa, trayecto entre Tauca y Maripa, 50-60 m, 27 Jul 1974 (fl), *Ruiz-Teran & Lopez-Palacios 11673* (K); Dist. Sucre, Orillas de la carretera Ciudad Bolívar-Maripa, trayecto entre Tauca y Maripa, 50-60 m, 27 Jul 1974 (fl, fr), *Ruiz-Teran & Lopez-Palacios 11675* (K); Municipio Asc. Farreras, 4°59’N, 60°10’W, 130 m, Mar 1990 (fl), *Sanoja & Elcoro 3446* (MO); Reserva Forestal Imataca, selva pluvial del medio río Botaramo, entre la pica de las minas y el río Guarampín, 18 Jan 1983 (fl, fr), *Stergios et al 5192* (MO); Dist. Cedeño, Bosque de galería del caño Chaviripa del drenaje del Escudo Guyanés, carretera Caicara-El Burro, 16 Apr 1984 (fl), *Stergios et al 8600* (MO); Hoja NB20-5, Serrania Maigualida, Frente 9, HP 1, al este del Río Caura, 7°5’30”N, 64°57’W, 100-180 m, 7 Apr 1989 (fr), *Stergios & Delgado 13627* (US); La Unión, Medio Caura, 80 m, 15 Feb 1939 (fl, fr), *Williams 11270* (US); En la orilla del Medio Caura, La Ceiba, 160 m, 13 Mar 1939 (fr), *Williams 11512* (F, US); Temblador, Medio Caura, 100 m, 20 Mar 1939 (fl, fr), *Williams 11547* (F, US); Temblador, Medio Caura, 100 m, 1 Apr 1939 (fl, fr), *Williams 11679* (F, US); La Paragua, 70 m, 15 May 1940 (fl), *Williams 12598* (F, US); San Mateo, en las orillas periodicamente anegadas del Río Paragua, 75 m, 9 Apr 1940 (fl, fr), *Williams 12818* (F, US); San Mateo, en las orillas periodicamente anegadas del Río Paragua, 70 m, 9 Apr 1940 (fl, fr), *Williams 12824* (F, US); En los conucos de El Tigre, cerca del Río Cuchivero, 90 m, 18 Jun 1940 (fl, fr), *Williams 13358* (F, US); Cuchiver, El Tigre, cerca del Río Cuchivero, 90 m, 18 Jun 1940 (fl, fr), *Williams 13361* (F, US); Orilla del Medio Orinoco, Caicara, 95 m, 12 Jun 1940

(fl, fr), *Williams 13282* (F, US); Piedra Marimare, east bank of Rio Orinoco, opposite head of Isla El Gallo, 19 Dec 1955 (fl), *Wurdack & Monachino 39988* (MO). **Delta Amacuro:** Caño ifarivsa, 23 Jul 1993 (fr), *Colonnello 1379* (MO); Dept. Tucupita, caño Jota-Sabuca, between Laguna del Sonsejo and Caño Mariusa, north of Río Grande of Río Orinoco, 8°43'N, 61°58'W, 50 m, 24 Oct 1977 (fl, fr), *Steyermark et al 115342* (MO). **Guárico:** Estero de Camaguán, parte baja, Apr 1971 (fl), *Aristeguieta 7799* (MO); Dist. Miranda, Parque Nacional Aguaro-Guariquito, Montaña de Guardahumo ca. 8°88'-8°92'N, 67°40'-67°44'W, 40-60 m, Dec 1981 (fl), *Delascio et al 11330* (MO); Dist. Miranda, Parque Nacional Aguaro-Guariquito, sabanas de Las Macanillas, Sur-este Montaña Guardahumo, ca 8°88'-8°92'N, 67°40'-67°44'W, 40 m, Dec 1981 (fl), *Delascio et al 11378* (MO); Dist. Infante, Penoía, margen izquierda del Río Ornioco, Parmana, Mcpo. Parmana, 19 Mar 1991 (fl), *Martino et al 329* (MO); 2 km west of San Fernando on Hato La Guanota, <100 m, 10 Dec 1982 (fl), *Rondeau 204* (MO); ca. 39 km south-southwestof Calabozo on Hato Masaguaral, 8.5°N, 67.5°W, <100 m, 19 Nov 1983 (st) *Rondeau 558* (MO); Hato Parmana, comisión Borrachera, 1955 (fr), *Tamayo 4044* (US). **unknown:** selvas pluviales en la orilla y sus alrededores del río Casiquiare entre la boca del Siapa y el caño Momoni, 18 Feb -4 Mar 1986 (fl, fr), *Stergios & Aymard 9170* (MO)

UNKNOWN LOCATION**:** no location (fl), *Schomburgk 113* (BM)

Solanum pedemontanum (10) M. Nee, Brittonia 58: 341. 2006. — TYPE: Ecuador. Napo: Añangu. Parque Nacional Yasuní, 0°31-32'S, 76°23'W, 30 May-21 Jun 1982 (fr), *B. Øllgaard et al. 39285* (Holotype: QCA!; isotype NY! [NY00711784]).

Vine 1-4 m. Stems sparsely to moderately armed with recurved, tan roselike prickles, these 1.5-3 mm long, the base 2-4 x 0.5-1 mm, moderately pubescent with tan to rusty, porrect-stellate hairs, the stalks absent to 0.5 mm, multiseriate, the rays 6-8, 0.2-0.8

mm, unicellular to multicellular, the midpoints nearly absent. Flowering portions of the stem consisting of difoliate sympodial units, the leaves usually geminate, those of a pair often slightly unequal. Leaves simple, the blades 5-16 x 2-5 cm, ovate, unlobed, chartaceous, discolorous, green to dark green adaxially, whitish-green abaxially, both leaf surfaces with stellate hairs like those of the stem but with the midpoints nearly absent to 1 mm, the adaxial surface sparsely pubescent, the abaxial surface moderately to densely pubescent with white to tan stellate hairs; major veins 4-8 on either side of the midvein, the midrib abaxially sparsely to moderately armed with recurved prickles like those of the stem but to 1.5 mm long; base obtuse, asymmetrical; apex acute; petioles 0.5-3 cm, moderately pubescent with stellate hairs like those of the stem, sparsely armed with prickles like those of the stem. Inflorescences 3-6 cm, extra-axillary, unbranched, with 3-12 flowers, the plants andromonoecious, with male flowers on young plants and hermaphroditic flowers on older plants, the axes moderately to densely pubescent with hairs like those of the stem, unarmed; peduncle 5-10 mm; rachis 2-4.5 cm; pedicels 5-10 mm in flower, 12-20 mm in fruit, curved, slightly expanded distally, spaced 1-2.5 mm apart. Calyx 2-4 mm long, the tube 2-4 mm, the lobes nearly absent to 0.5-1.5 x 0.5-1 mm, triangular, moderately pubescent with hairs like those of the stem, unarmed; fruiting calyx 4-6 mm, not accrescent in fruit. Corolla 2.5-5 cm in diameter, chartaceous, white, stellate, lobed nearly to the base, lacking interpetelar tissue, the lobes 10-25 x 2-4 mm, narrowly triangular, slightly reflexed at anthesis, moderately to densely pubescent abaxially with white to rusty stellate hairs like those of the stem but with midpoints to 1.5 mm, glabrous adaxially. Stamens 10-14 x 1-2 mm; filaments nearly absent to 1 mm, glabrous; anthers 10-13 x 1-2 mm, attenuate, tapering, connivent, yellow, the base cordate, the apex obtuse, the pores apical, directed slightly introrsely. Ovary glabrous to

sparsely pubescent with short, glandular hairs; style in functionally male flowers 4-7 x 0.5-1.0 mm, not exserted beyond stamens, cylindrical, glabrous, style in hermaphroditic flowers 12-16 x 0.5-1.0 mm, exserted beyond stamens, cylindrical, glabrous; stigma to 1.5 mm wide, capitate, green. Fruit a slightly leathery berry, 1-2 cm in diameter, globose, orange to red when mature, glabrous. Seeds 20-30 per fruit, reniform, brown, 2.5-3.5 x 2.5-3 mm, flattened, the surface netlike with many pits separated by small raised ridges (Fig. 4.21).

Habitat and distribution. (Fig. 4.22) Found on the eastern slopes of the Andes and adjacent Amazonian lowlands from Colombia to northern Bolivia and occasionally on the western Andean slopes in Ecuador at 100-1300 m.

Etymology. The epithet for this species was chosen to describe the distribution of this species along the piedmont of the eastern Andes and adjacent Amazon (Nee et al. 2006).

Notes. *Solanum pedemontanum* is a common species of the eastern Andean slopes and the adjacent Amazonian lowlands, however, like other members of the section, it is not found far into the Amazon Basin. The range of *S. pedemontanum* overlaps with that of *S. leucopogon* and the two are often found in close proximity at forest edges or gaps within the forest.

Because they are sympatric and have similar morphologies, comparisons of *S. pedemontanum* and *S. leucopogon* are inevitable. Both are vining species of light gaps and disturbed areas of the eastern slope of the Andes with similar floral morphologies including creamy white corollas, approximately 2.5 cm in diameter, strongly connivent yellow stamens, and temporally andromonoecious breeding systems. The fruits of both species are also similar and are orange to red, leathery berries. The most notable

difference between these species is the hair characteristics. The hairs of *S. pedemontanum* are generally white to tan and are stellate with 6-8 rays that are the same length as the midpoint. *Solanum leucopogon* is distinct with red hairs that have a greatly extended midpoint (1-5 (8) mm in length). The leaves of *S. leucopogon* are often lobed while those of *S. pedemontanum* are entire. Additionally, the calyx of *S. leucopogon* is much larger (5-10 mm in flower and 8-12 mm in fruit versus 2-4 in flower 4-6 in fruit mm in *S. pedemontanum*).

Phylogenetic results place *S. pedemontanum* sister to a clade composed of *S. volubile* and *S. aturense* but with weak support (>50% BS, 1.0 PP; Stern & Bohs, in prep). These latter two species are common throughout the Caribbean and reach into northern South America, however, they do not reach the range of *S. pedemontanum*. While the flowers of *S. aturense* are typically larger than those of *S. pedemontanum*, the flowers of *S. volubile* do overlap in size with *S. pedemontanum*. Perhaps the most obvious difference between these taxa lies in the cauline hairs, which are often long-stalked in *S. aturense* and *S. volubile* while they are nearly sessile to 0.5 mm in *S. pedemontanum*. Even in collections of *S. volubile* and *S. aturense* that have shorter-stalked hairs, the pale hairs of *S. pedemontanum* that often form a dense tomentum, especially on the abaxial leaf surface, are distinctive.

Additional specimens examined. BOLIVIA. **Santa Cruz:** Prov. Ichilo, Víbora, ca al Puente sobre el Río Chore, ca. 17°20'S, 63°55'W, 275 m, 9 Nov 1990 (fr), *Salidas, Penington, Johnson 1274* (K).

BRAZIL. **Acre:** Município de Rio Branco, Estrada Rio Branco Porto Acre km 33, a 2 km da margem, 12 Oct 1980 (fr), *Cid & Nelson 2883* (F, K, US); Boca do Acre-Rio Branco road, 14 km from Rio Branco, 27 Sep 1980 (fr), *Lowrie, Lowy, & Souza 228* (F).

Amazonas: Municipality São Paulo de Olivença, near Palmares, 11 Sep- 26 Oct 1936 (fl), *Krukoff 8421* (BM, F).

COLOMBIA. **Amazonas:** Mun. de Leticia, Parque Nacional Natural Amacayacu, Centro Administrativo Amacayacu-INDERENA, a la orilla del Río Amacayacu, 3°47'S, 70°15'W, 100 m, 9 Apr 1991 (fl), *Pipoly, Rudas, & Palacios 15152* (MO); Mun. de Leticia, Parque Nacional Natural Amacayacu, sector de Mata-Matá, a la orilla de la guebrada Bacaba, 3°47'S, 70°15'W, 100 m, 16 Apr 1992 (fr), *Rudas & Prieto 4278* (BM); Trapecio amazónico, Amazon watershed, Loretoyacu River, about 100 m, Mar 1946 (fr), *Schultes 7130* (GH).

ECUADOR. **Chimborazo:** Entre Bucay y Hcda. Rosa Mercedes, estrivaciones inferiores de Cord. Occ., 600 m, 12 Aug 1943 (fr), *Solís 5200* (F). **El Oro:** Pinas, Parroquia El Placer, Reserva Buenaventura, propiedad de la Fundacion Jocotoco, recorrido por el sendero desde la estacion hasta el bosque Puma, 3°38'41"S, 79°45'46"W, 1000 m, 4 Apr 2005 (fr), *Vargas, Defas, & Becerra 5176* (BM). **Esmeraldas:** San José, km 321 along railroad from Ibarra to San Lorenzo, 1°N, 78°W, 350 m, 4 May 1982 (fr), *Boom 1364* (K, US) **Morona-Santiago:** Pozo petrolero "Garza" de TENNECO, 35 km (aprox) al noreste de Montalvo, 01°49'S, 76°42'W, 260 m, 2-12 Jul 1989 (fr), *Zak & Espinoza 4448* (BM). **Napo:** Cantón Archidona, faldas al sur del Volcan Sumaco, carretera Hollín-Loreto, km 31, comuna Challua Yacu, 00°43'S, 77°36'W, 1200 m, 15-17 Nov 1988 (fr), *Alvarado 53* (F); Río Wais a ayá, 1 km upstream from the outlet in Río Aguarico, 76°21'W, 0°15'S, 300 m, 6 Aug 1981 (fr), *Brandbyge et al. 33229* (K); Yasuni scientific research station, Río Tiputini, northeast confluence with Río Tivacuno, 6 km east of Maxus road, km 44, off spur road to Tivacuno oilwell, by Maxus road near entrance to 50 hectare plot at km 6, 00°42'01"S, 76°28'05"W, 200-300

m, 3 Mar 1997 (fr), *Burnham 1453* (F); Orellana, Parque Nacional Yasuní, carretera y oleoducto de Maxus en construcción, km 5-28, 0°31'S, 76°32'W, 230 m, 23-27 May 1994 (fl), *Dik 1315* (BM); Road Coca-Auca oilfields, 3 km along the road to Yucca, 00°28'S, 76°55'W, 400 m, 20 Aug 1979 (fl), *Holm-Nielson, Jaramillo, & Coello 19635* (A, F); Yasuní National Park, by the Y between NPF and the Capiron oil well, 00°40'S, 76°25'W, 240 m, 14 Mar 1997 (fr), *Nabe-Nielsen 624* (BM); Vicinity of Puyo, eastern foothills of the Andes, 750-1000 m, Sep 1939 (fl), *Skutch 4545* (A, K). **Orellana:** Parque Nacional Yasuní, Estación Científica Yasuní, Río Tiputini, northwest of confluence with Río Tivacuna, east of Repsol-YPF road, km 7 along road to Tivacuna oil well, 00°38'S, 76°31'W, 200-300 m, 3 Feb 2000 (fl, fr), *Whitefoord, Garwood, & Persson 37* (BM), *45* (BM), *824* (BM). **Pastaza:** Along road from Mera to Río Anzu, 7.0 km N of Río Alpayacu, 1°25'56"S, 78°04'53"W, 1267 m, 8 May 2003 (fr), *Croat, Hannon, & Menke 88767a* (MO); Pastaza, Pozo Moretecocha, en el sitio de plataforma, 1°04'S, 77°25'W, 580 m, 23 Aug 1992 (fl), *Palacios 10383* (MO).

PERU. **Huánuco:** Pachitea, Codo de Pozuzo, floodpliain of Río Pozuzo after it emerges from mountains, trail to NW behind settlement, 9°40'S, 75°25'W, 450 m, 18 Oct 1982 (fr), *Foster 9259* (BM, F); Huánuco to Pampayacu, 13 Jan 1927 (fr), *Kanehira 189* (F). **Loreto:** Maynas, Dist.. Iquitos, Río Mamon, tributary of Río Nanay, ca. 150 m, 10 Dec 1976 (fl, fr), *Davidson & Revilla 5376* (F, US); Along Río Marañon, near mouth of Río Tigre, about 115 m, 19 Aug 1929 (fr), *Killip & Smith 27519* (US); Puerto Arturo, lower Río Huallaga below Yurimaguas, ca. 135 m, 24-25 Aug 1929 (fr), *Killip & Smith 27753* (US); Río Itaya, above Iquitos, about 110 m, 17-22 Sep 1929 (fl), *Killip & Smith 29389* (US); Mishuyacu, near Iquitos, 100 m, Feb-Mar 1930 (fl), *Klug 910* (F, US); Prov. Maynas, Dtto. Punchana, Río Momón, mouth to Porvenir, ca. 90 m, 10 Jan 1994 (fl, fr),

McDaniel & Rimachi 32105 (US); Prov. Maynas, Dtto. Iquitos, Río Itaya barredera de Pena Negra, 110 m, 6 Mar 1973 (fl), *McDaniel & Rimachi 16879* (US); Dtto. Tigre, Río Tigre, 2°33' S, 75°42'W, 18 Mar 1974 (fl), *McDaniel & Rimachi 18456* (US); Iquitos, Creek Itaya, 100 m, 6 Feb 1932 (fl), *Mexia 6485* (F, GH, K, US); Near Shiriara, Rio Nanay, 21 Feb 1969 (fl), *Plowman 2557* (K, US); Rio Javari, below mouth of Rio Curaça, 27 Oct 1976 (fl, fr), *Prance et al. 24160* (K, MO); Provincia Maynas, Distrito Pebas, Quebrada Shishita, 10 km de Pebas, 14 May 1976 (fr), *Revilla 609* (BM); Gamitanacocha, Río Mazán, 18 Jan 1935 (fl), *Schunke 77* (A, F, US); Maynas, orillas del Río Nanay más abajo del Puerto de Bellavista a 8 km, S.O. de la ciudad de Iquitos, 22 Nov 1965 (fl), *Torres 126* (ECON); Caballo-Cocha on the Amazon River, Aug 1929 (fl), *Williams 2479* (F); Alto Río Itaya, 145 m, Sep-Oct 1929 (fl), *Williams 3448* (F).

Solanum tampicense (11) Dunal**,** in DC., Prodr. 13(1): 284. 1852. **—** TYPE: MEXICO. Edo. Tamaulipas, Tampico, *J. Berlandier 185* (Lectotype, **here designated**: G!; isolectotypes: F! [F0073155F])

Solanum quercifolium Mill. Gard. Dict. ed. 8, no. 16. 1768. **—** TYPE: Grown in London from seeds from Mexico, Veracruz, *P. Miller s.n.* (Holotype BM! [BM000514917])

Solanum houstonii Dunal Hist. Solan. 243. 1813. — Type: Grown in London from seeds from Mexico, Veracruz, *P. Miller s.n.* (Holotype BM! [BM00514917])

Scandent shrub 1-2 m. Stems moderately to densely armed with recurved, yellow prickles, these 2-8 mm long, the base 2-5 x 0.5-1.5 mm, glabrous to sparsely pubescent with tan to rusty, porrect-stellate hairs, the stalks nearly absent to 0.5 mm, multiseriate, the rays 3-6, 0.5-1 mm, unicellular to multicellular, midpoints 0.5-1 mm. Flowering portions of the stem consisting of difoliate sympodial units, the leaves usually geminate,

those of a pair nearly equal. Leaves simple, the blades 4-16 x 2-6 cm, ovate, chartaceous, slightly discolorous, dark green adaxially, green to whitish green abaxially, the adaxial and abaxial surfaces sparsely pubescent with hairs like those of the stem; major veins 4-6 on either side of the midvein, the secondary veins obscure, the midrib adaxially occasionally with few straight prickles to 3 mm, the base 1.5-3 x 0.5-1 mm, the midrib abaxially with few to many recurved prickles like those of the stem; base acute and slightly decurrent onto the petiole; margin with 2-5 obtuse lobes per side, the sinuses cut less than 1/3 - 1/2 of the way to the midvein; apex acute; petioles 1-4 cm, adaxially moderately pubescent and abaxially sparsely pubescent with hairs like those of the stem, moderately armed abaxially, often with 2-ranked prickles like those of the stem. Inflorescences 1-4 cm, extra-axillary or leaf-opposed, unbranched, with 3-10 flowers, apparently all perfect, the axes sparsely pubescent with hairs like those of the stem, unarmed; peduncle 0.5-2 cm; rachis 0.5-3.5 cm; pedicels 0.5-2 cm in flower and fruit, nearly contiguous, spaced 0.5-2 mm apart. Calyx 2-5 mm long, the tube 1-2 mm, the lobes 1-3 x 0.5-2 mm, narrowly triangular, glabrous, occasional with recurved spines; fruiting calyx 4-7 mm, not accrescent in fruit. Corolla 1.5-2.0 cm in diameter, chartaceous, white to cream, stellate, lobed nearly to the base, lacking interpetaler tissue, the lobes 8-15 x 1-3 mm, narrowly triangular, moderately pubescent abaxially with white hairs like those of the stem, glabrous adaxially. Stamens 4-7 mm; filaments 2-3 mm long, glabrous; anthers 4-6 x 1-2 mm, attenuate, tapering, connivent in bud, spreading in flower, yellow, the base cordate, the apex obtuse, the pores apical, directed slightly introrsely. Ovary glabrous; style 4-6 x 0.5-0.75 mm, exserted beyond stamens, parallel or often perpendicular to stamens, cylindrical, white, glabrous; stigma to 1 mm wide, green, cylindrical. Fruit a thin-skinned berry, 5-8 mm in diameter, globose, green when

immature, red when mature, glabrous. Seeds 10-20 per fruit, reniform, brown, 1.5-2 x 1-1.5 mm, flattened, the surface netlike with many pits separated by small raised ridges (Fig. 4.23).

Habitat and distribution. (Fig. 4.17) Weedy species of swamps and wet areas from southern Florida and Mississippi through the Caribbean and Central America with occasional specimens from the Caribbean coast of Venezuela, at sea level to 150 (-700) m in elevation.

Etymology. The epithet refers to the location of the type collections, which were collected near Tampico, Estado Tamaulipas, Mexico.

Notes. *Solanum tampicense* is a found in lowland swamps from Mississippi and Florida through the Caribbean and Central America with one collection from northern Colombia and one from northern Venezuela. It appears to need constant water and is common along riverbanks or in swampy, marshy areas. It is not common in Florida but it is listed as an invasive species and noxious weed in Florida and where it does occur it forms impenetrable thickets. This dense growth coupled with the vicious prickles makes it a species of concern in the swamps of Florida.

The lobed leaves, nearly glabrous stems, spreading stamens, and style that is often exserted parallel to the stamens make *S. tampicense* easily distinguishable from other species. It is sympatric through much of its range with *S. aturense* and *S. volubile* but has nearly glabrous stems versus the typically moderately to densely hairy stems of the latter. *Solanum tampicense* also has smaller flowers (>2.0 cm in diameter versus < 2.0 cm in *S. aturense* and *S. volubile*) and smaller fruits (>8 mm in diameter versus < 10 mm in *S. aturense* and *S. volubile*).

Phylogenetic results strongly support (100% BS, 1.0 PP) *S. tampicense* as sister to *S. arachnidanthum* (Stern and Bohs in prep). Their morphological similarities are discussed above, however, from a biogeographical standpoint this is a surprising result as these two species occur at opposite ends of the range with *S. tampicense* at the northernmost extent and *S. arachnidanthum* at the southernmost.

In the description of *S. tampicense* Dunal lists collections of three specimens but none are designated as type. The collections of *Berlandier 48* were also used as type material for *S. enoplocalyx* var. *mexicanum* and are actually specimens of *S. lanceifolium*. The collection of *Berlandier 115* at G-DC is on the same sheet as that of *Berlandier 48*. To avoid confusion with these and because it is one of the best specimens, the collection of *Berlandier 185* at G was selected as the lectotype.

Additional specimens examined. BELIZE. **Belize:** Belize City, beach along Caesar Road, and road past city dump from Western Highway to Caeser Road, 24 Jun 1973 (fr), *Dwyer 11400* (F); Belize District, Belize-Sibun Road (fl, fr), *Gentle 60* (F); Belize City (map indicates east side of city near Caribbean), 1 m, 9 Aug 1992 (fl, fr), *Worthington 21436* (MO). **El Cayo:** El Cayo, Jun-Aug 1936 (fl), *Lundell 6111* (A, US) **No dept:** Yucatan Peninsula, northern River, Nov 1933 (fl, fr), *Gentle 875* (A, F, MO, US); River Ridge Plantation near Belize River, 11 miles from Belize on Northern Highway, near sea level, 25-26 May 1973 (fr), *Gentry 7596* (MO); Along the Western Highway, at about mile 14.5 at Hattieville, 3 Jun 1979 (fl, fr), *Harriman 16053* (US); Hattieville, Western Highway, edge of Hector Creek, 28 Mar 1970 (fl, fr), *McDaniel 13086* (MO); Near Manatee Lagoon, 2 Aug 1905 (fl, fr), *Peck 93a* (GH); Stann Creek Railway 11 mile, 15 Apr 1929 (fl, fr), *Schipp 171* (BM, F, G, GH, US); Malfodi Lagoon, 100 ft, 7 May 1934 (fl), *Schipp 1303* (A, BM, F, G, GH, MO).

COLOMBIA. **Bolivar:** Municipio San Martín de Loba, Pueblo Nuevo, alrededores de la Ciénaga el Totumo, camino al volcán de lodo, 10°8.73'N, 75°16.15W, 18 Feb 1989 (fl, fr), *Marulanda & Alba Rodríguez 843* (MO).

COSTA RICA. **Alajuela:** Vicinity of Los Chiles, Rio Frio, 11°02'N, 84°44'W, 30-40 m, 1 Aug 1949 (fr), *Holm & Iltis 652* (A); sin loc, Feb 1865 (fl, fr), *Wright 3028* (BM,G, K, W); Refugio Caño Negro, Los Chiles, San Carlos, 10°53'N, 84°47'W, 30 m, 8 Jul 1987 (fl, fr), *Zamora & Chacón 1343* (F, MO).

EL SALVADOR. **Ahuachapán:** A.P. Santa Rosa, ruta 6, 13°48'N, 90°04'W, 20 m, 15 Mar 2004 (fr), *Rosales 2244* (BM). **La Libertad:** San Diego, El Amatal, 13°29'N, 89°10'W, 3 m, 14 Dec 1997 (fr), *Aparicio & Hernandez 96* (MO); San Diego, El Amatal, 30 Mar 1993, (fl), *González 153* (MO); El Amatal, 13°29'N, 89°17'W, 26 Jun 1992 (fl), *Villacorta & González 1130* (MO). **Sonsonate:** Vicinity of Acajutla, 30 m or less, 20 Mar 1922 (fr), *Standley 21918* (GH, US).

GUATEMALA. **Escuintla:** Near San José, sea level, 30-31 Jan 1939 (fl), *Standley 64257* (F).

HONDURAS. **Atlantida:** Laguna de Los Micos, NW of Tela, up river 0.5 km W of Miami, 15°50'N, 87°36'W, 1-2 m, 10 Nov 1988 (fl, fr), *MacDougal, House, & Zúniga 3440* (F, MO). **Comayagua:** Río Tepemechin, 1 km south of Lago de Yojoa, 19 May 1987 (fl), *Blackmore & Chorley 3956* (BM, MO).

MEXICO. **Campeche:** Mun. Ciudad del Carmen en Finca Mamantel, sobre el Río Las Cruces, en el sistema pluvio-lagunar del Río Palizada, 25 Nov 1987 (fl), *Cabrera & Cabrera 14962* (MO); Palizada, 25-28 Jul 1939 (fl, fr), *Matuda 3883* (F, GH); Municipio Carmen, carretera Champotón-Isla Aguada, km 90, dirección W, 18°53'30"N, 91°24'10"W, 10 m, 27 Sep 1984 (fl, fr), *Ortiz 675* (BM). **Chiapas:** Río Salinas, below

Río Pasion, 9 Feb 1964 (fl, fr), *Lundell 17885* (F, MO); A 3 km al E de Pico de Oro, camino Benemérito de las Américas, Mpio, Ocosingo, 180 m, 18 Apr 1986 (fl, fr), *Martínez 18394* (MO); En Crucero Corozal, sobre el camino Palenque-Boca Lacantum, Mpio. Ocosingo, 250 m, 29 Jun 1986 (fr), *Martínez 19127* (MO). **Guerrero:** Laguna de Coyuca, cerca de Pie de la Cuesta, municipio de Acapulco, 0 m, 6 Jul 1966 (fl, fr), *Rzedowski 22708* (F) **Nayarit:** Mun. Santiago Ixcuintla, a 10 km al W de Union de Corrientes, camino a Mezcaltitan, 40 m, (fr), *Tellez & Salinas 12118* (MO) **Tabasco:** Las Estacas, a 3 km de la 15 y 2 km de la 10, en Balancan, 28 Oct 1975 (fr), *Novelo et al 11* (MO); Reserva dela Biósfera Pantanos de Centla, Calzada del Arroyo Tabasquillo, a 6.7 km de la Etación Tres Brazos, Mpio Centla, 18°22'12"N, 92°40'34"W, 8 m, 27 Nov 2001 (fl), *Novelo et al 4267* (MO); 22 km W traffic circle Villahermo along Mex 180, 20 Jun 1971 (fl, fr), *Spellman et al 124* (MO); 22 km W traffic circle, Villa Hermosa, 20 Jul 1971 (fl, fr), *Spellman et al 117A* (MO); Mpio. Nacajuca, Loc. Campo Sen, Río González, 18° 8'N, 92°54'W, 15 Jun 1997 (fr), *Tenorio et al 19595* (MO); San Roman, Mpio. Villa Hermosa, sea level, 21 Jun 1984 (fr),, *Ventura 21127* (F, MO) **Veracruz:** En la Congregación de Barra de Palmas, 20°10'N, 96°44'W, 20 m, 21 Aug 1978 (fl, fr), *Calzada 4736* (F); Orillas de la Laguna de la Mancha, Actopan, 0-5 m, 4 Dec 1975 (fl, fr), *Dorantes et al. 5343* (F); La Purga, 27 Jan 1906 (fl, fr), *Greenman 264* (F, GH, US); Pantanos cerca de Lerdo de Tejada Rumbo Alvarado, 50 m, 15 Mar 1971 (fr), *Lot 1287* (F, GH); Cerca de la desembocadura de Río Papaloapan, mapa 55 E 9, 5 m, 31 Oct 1971 (fl, fr), *Lot 1533* (MO); Río Huezatlan Viejo, Laguna el Ostion, mapa 71/F5, 0 m, 19 Dec 1971 (fl, fr), *Lot 1668* (MO); Along the highway following the Río Papaloapan towards the coast, 2 km NE of Tlacotalpan, Mun. Tlacotalpan, 18°38'N, 95°39'W, 2 m, 8 Apr 1983 (fl), *Nee & Taylor 26544* (F, MO); Along hwy. Mex 150 and 180, 1.5 km SW of

bridge at Boca del Río, Mun. Boca del Río, 19°05’30”N, 96°07’W, <5 m, 22 Feb 1984 (fr), *Nee & Taylor 29614* (F, MO); Tlacotalpan, 21 May 1894 (fl, fr), *Nelson 501* (US); 4km al sur de Playa Vicente, Rumbo a Nigromante, 95 m, 12 Apr 1969 (fr), *Nevling & Gomez-Pompa 836* (GH); Vicinity of Pueblo Viejo, 2 km south of Tampico, 23-31 May 1910 (fl, fr), *Palmer 422* (GH, MO). **Yucatán:** Municipio Celestún, 35 km al oeste de Kinchil, unos 6-8 km al E de la Ría de Celestún, a lo large de la carrereta Mérida-Celestun, aprox. 20°51’06”N, 90°17’00”W, 0-5 m, 10 Jun 1999 (fr), *Carnevali, May, & Tapia 5555* (F).

PANAMA. **Chiriqui.** South of David near Pedregallto, 26 Oct 1983 (fl), *Schmalzel 1835* (MO).

UNITED STATES OF AMERICA. **Florida:** Highlands Co., Fisheating Creek, crossing at FL731, W. of Venus, next to Florida Audobon Society land, 27°03’58.0”N, 81°25’27.4W, 14 Apr 2007 (fl, fr), *Bohs & Stern 3655* (UT); Highlands Co., east side of Fisheating Creek at county road 731, about 10 mi W of US hwy. 27, 26 May 1993 (fl), *Coile et al. 4940* (FLAS); Highlands Co., S of FL 8 along Fisheating Creek, 21 Dec 1992 (fl, fr), *DeLaney 1922* (FLAS); Orange Co., near Boggy Creek, settlement 6 mi SE of Taft, 9 Dec 1930 (fr) *Nicholson 103* (US); Monroe Co., Dry Tortugas National Park, Garden Key, interior of the Little Magazine, 25 Feb 1997 (fl), *Reimus & Robertson 1088* (FLAS); Desoto Co. off state rd. 70, in Arcadia, along Peace River, 18 Jun 1993 (fr) *Runnals s.n.* (FLAS).

VENEZUELA. **Bolivar:** Rio Paragua, hasta 12 vueltas arriba de la boca del Rio Tonoro, 6°3’N, 63°57’W, 175 m, 13 Jun 1987 (fr), *Stergios 10329* (MO).

WEST INDIES. **Cuba. Camaguey:** Vicinity of La Gloria, 28 Jan 1909 (fl), *Shafer 97* (US). **Havana:** Laguna Briguanabo, 16 Apr 1922 (fl), *Ekman 13719* (G); Laguna de

Castellano, 27 Dec 1910 (fl), *Wilson 9556* (K). **Isla de Pinos:** near Nueva Gerona, 11 Apr 1904 (fl, fr), *Curtiss, 440* (BM, G, K, M, MO, US); Isle of Pines, about 2 km due N of Nueva Gerona, 6 Feb 1953 (fl, fr), *Killip 42629* (US); At end of road due N from Hotel Isle of Pines, Nueva Gerona, 28 Mar 1954 (fl, fr), *Killip 43774* (US); Habana, 2 km N of Nueva Gerona, Isla de Pinos, sea-level, 6-10 Feb 1956 (fr) *Morton 9988* (US). **Oriente:** Manzanillo, Sabana lamar ad marg. stagni., 24 Apr 1915 (fl, fr), *Ekman 5639* (G). **Pinar del Rio:** Vicinity of Los Palacios, 3-4 Jan 1912 (fl, fr), *Shafer 11670* (US). **Unknown Prov:** Cuba, 1860-1864 (fl, fr), *Wright 3028* (G, MO, US). **Villa Clara:** Santa Clara, Cienfuegos, Abreus, Rio Damuji (fl, fr), *Combs 228* (K, MO, US). **St. Lucia.** sin loc, 1854 (fr), *Anderson sn* (MO). **Grand Cayman:** Jan 1891 (fr), *Hitchcock s.n.* (MO).

Solanum volubile (12) Sw., Fl. Ind. Occ. 1: 458. 1797. *Solanum lanceifolium* Jacq. var. *volubile* (Sw.) Sendtn., in Martius Fl. Bras. 10: 109. 1846. — TYPE: WEST INDIES. *Swartz s.n.* (lectotype, **here designated,** BM! [BM000815975]; isolectotypes (possibly BM! [BM000886692], S))

Solanum adhaerens Roem. & Schult. Syst. 4: 669. 1819. — TYPE: VENEZUELA, D.F., Caracas. 1799-1800, *A. humboldt & A. Bonpland s.n.* (holotype B-W! [04406-010])

Solanum enoplocalyx Dunal, in A. DC., Prodr. 13(1): 222. 1852. —TYPE: MEXICO ["Peru, *Pavón*" *s.n.*], *M. Sessé & J. Moçiño s.n.* (holotype G-BOIS; isotypes, F (fragment), MA "*M. Sessé & J. Moçiño 1537*, MA "*M. Sessé & J. Moçiño 5352*", photo of MA isotype 1537 [F neg. 48290]: F!, photo of MA isotype 5352 [F neg. 48291]: F).

Solanum humboldtii Dunal var. *diacanthum* Dunal, in A. DC., Prodr. 13(1): 216. 1852. — TYPE: COLOMBIA. prob. Depto. Magdalena, Santa Martha, *C. Bertero s.n.* (holotype G-DC!, photo of holotype [F neg. 6825]: F!).

Solanum purulense Donn. Sm., Bot Gaz. 52: 52. 1911. —TYPE: GUATEMALA. Depto. Baja Veracruz, 1600 m, Apr 1907, *H. von Tuerckheim II 1751* (lectotype, **here designated,** US! [1324729]).

Names associated with this species that have not been validly published: *Solanum donnellsmithii* J. M. Coult., in J. D. Smith, Enum. Pl. Guatem. 2: 51. 1891.

Scandent shrub to woody vine 1-4 m. Stems moderately to densely armed with recurved, tan to orange roselike prickles, these 2-10 mm long, the base 1-7 x 0.5-1.5 mm, moderately pubescent with tan to rusty, porrect-stellate hairs, the stalks 0.5-3 mm, multiseriate, the rays 3-8, 0.5-1 mm, unicellular to multicellular, the midpoints nearly absent. Flowering portions of the stem consisting of difoliate sympodial units, the leaves usually geminate, those of a pair often unequal. Leaves simple, the blades 4-15 x 1-7 cm, ovate, leaves chartaceous, slightly discolorous, dark green adaxially, green to whitish green abaxially, the adaxial surface sparsely to moderately pubescent with stellate hairs like those of the stem but with the stalks to 0.5 mm and the midpoints to 0.5 mm (2-3 mm in some specimens from Trinidad), the abaxial surface moderately pubescent with stellate hairs like those of the stem; major veins 4-7 on either side of the midvein, the secondary veins obscure, the midrib abaxially with a few to many recurved prickles like those of the stem; base acute, often asymmetrical; margin with 2-4 obtuse lobes per side, the sinuses cut less than ¼ of the way to the midvein; apex acute; petioles 0.5-2.5 cm, moderately pubescent with hairs like those of the stem, moderately armed with prickles like those of the stem. Inflorescences 2-6 cm, extra-axillary, unbranched, with 5-15 flowers, the plants andromonoecious, with male flowers on young plants and hermaphroditic flowers on older plants, the axes moderately to densely pubescent with hairs like those of the stem, unarmed; peduncle 0.5-1.5 cm; rachis 1.5-4.5 cm; pedicels 5-10 mm in flower, 10-20 mm

in fruit, filiform, contiguous throughout, spaced 1-3 mm apart. Calyx 3-5 mm long, the tube 1-2 mm, the lobes 1-2 x 0.5-1 mm, triangular with acute apices, often recurved, moderately pubescent with hairs like those of the stem, occasionally with prickles 1-2 mm in length, straight to recurved; fruiting calyx 3-6 mm, not accrescent in fruit. Corolla 2-3 cm in diameter, chartaceous, white to cream with occasional purple lines, stellate, lobed nearly to the base, the lobes 10-15 mm x 1.5-3.5, narrowly triangular, slightly reflexed at anthesis, densely pubescent abaxially with stellate hairs like those of the stem but with 5-8 rays, these appearing partially proximally fused, adaxial surface glabrous. Stamens 10-13 mm; filaments 1-2 mm long, glabrous to moderately pubescent; anthers 8-12 x 1-2 mm, attentuate, tapering, connivent in bud, connivent to spreading in flower, yellow, the base cordate, the apex obtuse, the pores apical, directed slightly introrsely. Ovary moderately pubescent with white hairs like those of the stem; style in functionally male flowers 2-3 x 0.5-1.5 mm, style in hermaphroditic flowers 10-13 x 0.5-1 mm, exserted beyond the stamens, cylindrical, white, sparsely pubescent; stigma to 1 mm wide, cylindrical, green. Fruit a leathery berry, 10-20 mm in diameter, globose, green when immature, orange when mature, glabrous to very sparsely pubescent. Seeds 20-30 per fruit, reniform, brown, 2-2.5 x 1.5-2 mm, flattened, the surface netlike with many pits separated by small raised ridges (Fig. 4.24).

Habitat and distribution. (Fig. 4.25) Weedy species of forest edges, light gaps, and roadsides from Veracruz, Mexico through Central America and the northern coast of South America in Colombia, Venezuela, Guyana, and French Guiana and Trinidad and Tobago, commonly at sea level to 500m (1600 m).

Etymology. The etymology of *S. volubile* is unclear; it is possible that it is from the Latin “volubil-” meaning “turning” referring to the twining, scandent growth form.

Notes. The morphological characteristics of *S. volubile* are similar to *S. aturense* with which it is sympatric in much of its range. There is much morphological overlap between these species and viewing an individual specimen without additional material for comparison makes identification difficult. In general, *S. volubile* is characterized by leaves that are chartaceous, often lobed and lacking a revolute margin, and only sparsely or moderately pubescent abaxially, whereas leaves of *S. aturense* are thick and somewhat coriacsous, not lobed and frequently have a revolute margin, and are often densely pubescent abaxially. Additionally, *S. volubile* has smaller flowers (2-3 cm in diameter versus 3-4 cm in *S. aturense*), smaller fruits (1-2 cm versus 1.5-3.5 in *S. aturense*) and smaller seeds (2-2.5 x 1.5-2 mm versus 3-3.5 x 2-2.5 mm in *S. aturense*). Due to their similar morphologies, it is unsurprising that *S. volubile* is strongly supported (100% BS, 1.0 PP) as sister to *S. aturense* in phylogenetic results (Stern and Bohs in prep).

We have designated the lectotype of *S. volubile* at BM as this is the only known specimen, although there is possibly a collection at S where Swartz was based. The description of *S. purulense* did not specify a holotype so we have lectotypified the collection at US, as it is the only known collection and is excellent material. The name *S. donnell-smithii* is a nomen nudum and appears to simply be a copy of his collection labels.

Additional specimens examined. BELIZE. **Belize:** Bermudian Landing, 17°34'N, 88°32'W, 27 Mar 1990 (fl, fr), *Arvigo et al. 362* (US); Bermudian Landing, Belize River, 25 May 1981 (fr), *Whitefoord 3027* (BM). **Cayo:** North of the Belize River near Spanish Lookout, 250 ft, 27 Nov 1968 (fl), *Proctor 29468* (BM). **Stann Creek:** Dangriga, near town along Melinda Road, 16°58' N, 88°14' W, 26 Nov 1990 (fr), *Balick et al. 3018* (US); Stann Creek, 12 Dec 1931 (fl, fr), *Schipp 849* (A, BM, G, GH, K). **Toledo:** San

Miguel Village Road, 16°18'N, 88°56'W, 11 Aug 1991 (fl), *Arvigo et al. 575* (US). **No dept:** Swasey Branch, Monkey River, 23 Oct 1941 (fl, fr), *Gentle 3722* (A, F); Little Cocquericot, Belize River, 25 Mar 1933 (fl), *Lundell 4001* (F, US); Near Manatee Lagoon, 2 Feb 1906 (fl), *Peck 324* (GH, K).

COLOMBIA. **Antioquia:** Near Río León approx. 20-30 km upstream and south of the river mouth and approx. 15 km W of Chigorodó, ca. 7°45'N, 76°50'W, less than 100 m, 20 Mar 1962 (fl), *Feddema 1978* (US). **Atlantico:** Barranquilla, Dec 1926 (fl, fr), *Bro. Paul C-12* (US); Las Flores near Barranquilla, Jan 1932 (fl, fr), *Bro. Paul 940* (F, US); Usiacurí, Hacienda "Cachubana", 50-60 m, 10 Jan 1940 (fl), *Dugand & Barriga 2376* (US); Entre Leña y Candelaria, 30-50 m, 11 Jan 1941 (fl, fr), *Dugand & Jaramillo 2774* (US); same loc. (fl, fr), *Dugand & Jaramillo 4115* (US). **Bogota:** Bogota, Bowman, Oct 1974 (fl), *Saunders sn* (K). **Bolívar:** Buenavista, east of Since, 100-150 m, 24 Jan 1918 (fl), *Pennell 3984* (GH, US); Los Volcanes, near Turbaco, 200-300 m, 12 Nov 1926 (fl), *Killip & Smith 14454* (A, GH, US); En la region del Sinú, cerca a la Hacienda "Martinica" a 15 km de Montería, ca. 30 m, 7 Jan 1949 (fl, fr), *Zainúm et al 19* (US). **Boyacá:** Opposite Rondon (formerly El Padre) on Boyaca-Arauca boundary, +/- 200 m, 14 Mar 1939 (fl), *Haught 2672* (US). **Cordoba:** El Cerrito, 10 km SE of Monteria, 12 m, 2 Nov 1969 (fl, fr), *Anderson 1857* (K). **Magdalena:** Región del Campano, Sierra Nevada de Santa Marta, ca. 1300 m, 11 Jan 1948 (fl), *Barkley & Gutiérrez 1888* (US); Alto de Mirador, Sierra Nevada de Santa Marta, 10°65'N, 73°50'W, 1200 m, 11 Mar 1992 (st) *Gentry & Saenz 76261* (MO); Isla de Salamanca, de los Cocos al Kilómetro cerro, por el Caño Clarín Nuevo, 29 Jul 1971 (fl, fr), *Romero-Castañeda & Núñez 11077* (F). **Meta:** Banks of Río Negrito, between Villavicencio and Puerto Lopez, 400 m, 13 Oct 1938 (fl), *Cuatrecasas 3543* (F, US); Río Meta, El Porvenir, 145 m, 16 Oct 1938 (fl),

Cuatrecasas 3683 (US); Int. del Meta, Puerto Lopez, 300 m, 29-30 Jul 1946 (st), *Jaramillo et al. 397* (US). **Norte del Santander:** Cordillera Oriental, region del Sarare, El Banco, confluencia de los ríos Cubugón y Cobaría, 320 m, 15 Nov 1941 (fr), *Cuatrecasas 13154* (US). **Santa Marta:** St. Martha (fl, fr), *Bertero 2615* (M); Río Frio, Jul 1925 (fl), *Walker 1283* (US). **Santander:** Vicinity of Puerto Berrio, between Carare and Magdalena Rivers, 100-700 m, 11 Jun 1935 (fl), *Haught 1770* (F, US); same loc., 31 Jul 1974 (fl, fr), *Haught 1974* (A, F); Puerto Wilches and vicinity, 100 m, 28 Nov- 2 Dec 1926 (fl), *Killip & Smith 14769* (GH, US). **Sucre:** Mun. Tolú, arroyo Palo Blanco, 7.5 km Tolú-Coveñas, litoral Caribe, Golfo de Morrosquillo, 9.4-9.5° N, 75.6-75.7° W, 0-5 m, 18 Sep 1990 (fl), *Betancur & Berrio 1957* (US). **Tolima:** Espinal to Cuamo, 350-400 m, 21 Jul 1917 (fl), *Pennell & Rusby 190* (GH, US). **No dept:** North Coast of Colombia, Panama, 1832 (fl), *Cuming 1134* (BM).

COSTA RICA. **Alajuela:** Vicinity of Los Chiles, Rio Frio, 11°02'N, 84°44'W, 30-40 m, 1 Aug 1949 (fl, fr), *Holm & Iltis 638* (A, G). **Guanacaste:** Casi en la division continental, cerca del Paso de El Silencio, 900 m, 6 Dec 1963 (fl), *Jiménez 1366* (F). **Heredia:** 1.4 km east of Puerto Viejo near Rio Sarapiqui, 75 m, 14 Jun 1966 (fl), *Anderson & Mori 2* (F); Near the Puerto Viejo, about 2 km upstream from the confluence with the Río Sarapiquí on the O.T.S. La Selva Research Area, 10°26'N, 84°0'W, 100-200 m, 26 Apr 1973 (fl, fr), *Gentry & Burger 3022* (F); Muelle, approx. 10°30'N, 84°0'W, 30 m, 22 Feb 1971 (fl, fr), *Nee & Mori 3507* (F). **Limón:** Limón, no protegida, Cuenca del Estrella, 9°40'30"N, 83°00'20"W, 200 m, 27 Jul 2000 (fr), *Acosta et al 1927* (G); Between Siquerres and the Río Pacuare and the remnant forest on steep hills south of the railroad bridge over the Río Pacuare, 10°05'N, 83°29'W, 50-100 m, 20-22 Dec 1969 (fl, fr), *Burger & Liesner 6867* (F); Hills between BriBri on the Río Sixaola and the

Caribbean Coastal Plain, 9°37'N, 82°49'W, 50-100 m, 10 Feb 1977 (fl), *Gentry 3725* (F); Unos 2 km al NE de la Estación Experimental Agricola de Diamantes, Guápiles, 260 m, 18 Sep 1964 (fl), *Jiménez 2344* (F, US); Puerto Limón, roadside near beach, just N of town, 12 Sep 1963 (fl, fr), *Porter 1128* (GH); Goldengrove, drenaje de Río Reventazón, 15 m, 23 Oct 1951 (fl), *Shank & Molina 4369* (F, GH). **Puntarenas:** Near Quepos and the Río Naranjo, 9°27'N, 84°08'W, 20-150 m, 18 Feb 1977 (fl, fr), *Gentry 3760* (F); Garabito, no protegida, Cuenca del Tulín, hotel de bosque situado al NW del hotel principal, 9°42'10"N, 84°39'20"W, 57 m, 30 Oct 2001 (fl), *Murillo et al 136* (G); North end of Golfito bay, 2 m, 5 Mar 1971 (fr), *Nee & Mori 3551* (F); Rincon de Osa, near Gulfo Dulce north of boat landing, 0-5 m, 20 Jul 1974 (fl, fr), *Utley & Utley 1079* (F). **San José:** Acosta, Sababillas, area no protegida, Soncuano, 9°40'11"N, 84°88'00"W, 1090 m, 31 Oct 2001 (fl), *Quesada et al. 795* (K). **No Dept:** Along the Río Barú near Dominical on the Pacific Coast, 9°17'N, 83°52'W, 0-20 m, 20 Feb 1977 (fl, fr), *Gentry 3774* (F); Hojancha de Nicoya, 200 m, 29 Jan 1942 (fl), *León 940* (F).

EL SALVADOR. **Ahuachapán:** San Francisco Menéndez, El Corozo, Mariposario, zon alta "Las Peralta", 13º49'N, 89º59'W, 325 m, 4 May 2000 (fr), *Rosales 660* (BM). **La Libertad:** Finca Germania near Comasagua, 900 m, 22 Jan 1946 (fl), *Carlson 204* (F). **La Paz:** 1923 (fl), *Choussy 50* (US). **San Salvador:** San Salvador, Nov 1921 (fl), *Calderón 86* (GH, US). **San Vicente:** Vicinity of San Vicente, 400-500 m, 7-14 Feb 1947 (fl, fr), *Standley & Padilla 3587* (F). **Sonsonate:** Balneario de Atecozol, 250 m, 20 May 1963 (fl), *Molina & Molina 12470* (F); Vicinity of Nahulingo, about 220 m, 21 Mar 1922 (fl), *Standley 22049* (GH, US).

FRENCH GUIANA: Riv. Mana, entre Saut Tamanoir et Saut Dalles, 17 Jul 1981 (fl), *Cremers 7208* (BR, MO).

GUATEMALA. **Alta Verapaz:** Near the Finca Sepacuite, 26 Mar 1902 (fl), *Cook & Griggs 162* (US). **Baja Verapaz:** wald bei Purulhá, 1650 m, Oct 1912 (fl, fr), *Türckheim 3982* (M, M, M, US). **Escuintla:** Río Guacalate, about 600 m, 16 Dec 1938 (fl), *Standley 60148* (F); Concepcion, 1200 ft, Apr 1890 (fl), *Tonduz & Rojas 83* (G, US). **Izabel:** Los Amates, 9 May 1919 (fl), *Blake 7330* (US); Puerto Mendez, on new Izabel road, 2 km 500 m from the village, 19 Oct 1969 (fl), *Contreras 8982* (F); Río Chacún, 100 ft, 10 Feb 1921 (fl), *Johnson 1230* (US); Morales, 8 Mar 1907 (fl, fr), *Kellerman 6086* (US); Vicinity of Quirigua, 75-225 m, 15-31 May 1922 (fl), *Standley 23768* (GH, US). **Jutiapa:** Near El Molino (Dept. Santa Rosa), about 600 m, 26 Nov 1940 (fl), *Standley 78461* (F). **Mazatenango:** Los Animas, 650 ft, Sep 1891 (st) *Civitt 623* (US). **Petén:** Sayaxche, on peninsula, in front of hotel, 13 Mar 1964 (fl, fr), *Contreras 4033* (F). **Quezaltenango:** Río Ocosito, 250 ft, Apr 1892 (fl, fr), *Donnell Smith 2672* (US). **Retalhuleu:** San Felipe, 2050 ft, Apr 1892 (fl), *Donnell Smith 2670* (F, G, G, GH, K, M, US); Near Nueva Linda, halfway between Retalhuleu and Champerico, 120 m, 26 Feb 1939 (fl), *Standley 66541* (F). **San Marcos:** Volcán Tajumulco, finca el Porvenir, 14°57'N, 91°56'W, 1500 m, 4 Sep 1999 (fl), *Morales 532* (F); Above Finca El Porvenir on "Todos Santos Chiquitos" lower south-facing slopes of Volcán Tajumulco, 1300-1500 m, 7 Mar 1940 (st) *Steyermark 37228* (F). **Santa Rosa**: Santa Rosa de Lima, colectado en Laguna de Pereira, 14°23'N, 90°17'W, 950 m, 23 Oct 1994 (fr), *Castillo & Luarca 2293* (F); Above Guazacapán, 220 m, 29 Nov-3 Dec 1940 (fr), *Standley 79052* (F). **Sololá:** South-facing slopes of Volcán Atitlán, above Finca Moca, 1000-1250 m, 20 Jun 1942 (fl), *Steyermark 47939* (A). **Suchitepéquez:** Near Patulul, 330-600 m, 5 Jan 1939 (fr), *Standley 62140* (F).

GUYANA. **Upper Demerara-Berbice:** Essequibo River, east bank, 5 km north of Bartica, 6°27'N, 58°35'W, 5 m, 18 May 1993 (fr), *Henkel & Williams 2085* (BM, US).

HONDURAS. **Atlántida:** Lancetilla Valley, 22 Jun- 27 Jul 1929 (fl, fr), *Chickering 221* (F); Lancetilla Jardon Botánico, 7 km SE de Tela, 8 Mar 1986 (fl), *Rodríguez 321* (F); Vicinity of San Alejo, 150-270 m, 22-27 Apr 1947 (fl), *Standley 7713* (F); Vicinity of La Ceiba, foothills back of Ceiba, 5 Jul 1938 (fl), *Yuncker et al. 8206* (F, G, GH, K, MO, US). **Colón:** Old airport road to Castillo, 3 km east of Trujillo, 9 Jun 1980 (fl, fr), *Saunders 313* (F). **Comayagua:** Las Limas, 3000 ft, 20 Jun 1932 (fl), *Edwards 330* (A, F, K, US). **Cortes:** Matorrales de San Jose, 5 kms al sureste de San Pedro Sula, 80 m, 20 Apr 1956 (fl, fr), *Molina 6750* (F). **El Paraíso:** Rio Guayambre 10 km south of Azuacalpa, 24 Feb 1982 (fl, fr), *Blackmore & Heath 1888* (BM); Vicinity of Danlí, 700-800 m, 11-23 Feb 1949 (fl), *Standley 16430* (F). **Morazán:** Lancetilla, 80 m, 26 Jul 1948 (fl), *Williams & Molina 14445* (F) **Olancho:** Catacamas, roadside between Rio Tinto and Catacamas, at bridge, 12 Sep 1991 (fl), *Chorley 218* (BM, BR). **Yoro:** Ocotales pedrejosas de Peidra Colorada, 1100 m, 10 May 1956 (fl), *Molina 6891* (F, US).

MEXICO. **Campeche:** 12 km antes de llegar al límite del Estado de Campeche con Tabasco, 17º59'55"N, 91º41'00"W, 8 m, 17 Feb 1986 (fl), *Chan 6118* (F). **Chiapas:** Near Chicharras, 6000 ft, 12-15 Feb 1896 (fl), *Nelson 3812* (GH, US); El Edén, municipio de Tapachula, 450 m, 18 Feb 1985 (fl), *Ventura 1161* (G). **Oaxaca:** District of Tuxtepec, Chiltepec and vicinity, about 20 m, Jul 1940- Feb 1941 (fr), *Martínez-Calderón 95* (A, US); Mun. Putla, Loc. Dto. Putla, 4 km al E de Santiago Yosotiche (Vado), entrando por Concepción Progreso, 16 Dec 1985 (fr), *Torres 8035* (M). **Tabasco:** Mpio. Teapa, 0.34 km al E de la Universidad Autónoma de Chapingo, 17º31'31"N, 92º55'33"W, 200 m, 5 Feb 2002 (fl), *Calónico 21498* (BM); 13 mi. E of the

Tabasco-Veracruz border at Río Tonalá along Mexican Hwy. 180, ca. 20 m, 5 Jun 1973 (fl, fr) *Hansen et al. 1709* (US). **Veracruz:** Pizapan 8 km al sur de San Andres Tuxtla, 18º23'N, 95º17'W, 25 Dec 1972 (fl, fr), *Calzada 907* (F); Mun. Cosamaloapam, Tres Valles, 24 Jul 1969 (fl), *Calderón 1949* (F); Tributary od Río Tonala, 2 km W of bridge over Río Tonala (border of Estado de Verecruz and Tabasco) near Las Choapas turn off, ca. 43 km E of Coatzocoalcos, 20 m, 17 Dec 1972 (fl), *Iltis 27256* (US); El Pital, Apr 1841 (fl, fr), *Liebmann 1435* (US, W); South edge of Tesechoacán, W side of Río Tesechoacán (=Río Playa Vicente, Mun. Villa Azueta, 18°07'30"N, 95°39'30"W, 50 m, 6 Dec 1981 (fl), *Nee 23824* (F); Along Río Tepango ("Río Grande") at highway bridge, 3 km SW of junction with Hwy. Mex. 180 in Santiago Tuxtla, 18°27'N, 95°19'W, 160 m, 5 Apr 1983 (fr), *Nee & Taylor 26493* (F).

NICARAGUA. **Chontales:** San Miguelito, drenaje del Lago Granada, 30 m, 13 Nov 1951 (fl), *Shank & Molina 4507* (F); Vicinity of Juigalpa, about 160 m, 4-12 Jun 1947 (fr), *Standley 9234* (F). **Managua:** Vicinity of Managua, Apr 1932 (fr), *Garnier 1034* (US). **Matagalpa:** Finca La Erida, zona de potreros y melezas, 13º01'N, 85º47'W, 550 m, 20 Jan 1982 (fl), *Castro 2324* (MO). **Zelaya:** Vicinity of La Luz-Siuna, north and northeast of La Luz, 150-200 m, 11 Mar 1961 (fl, fr), *Bunting & Licht 524* (F); Corn Island, 0-5 m, 7 Mar 1971 (fl), *Nelson 4345* (GH). **No dept:** Northeast Nicaragua, Region of Braggman's Bluff, 4 Jan 1928 (fl), *Englesing 111* (F, US); San Carlos, Jan 1893 (fl), *Shimek & Smith s.n.* (F); San Juan del Norte, Graytown, Nov 1895 (fl), *Smith 81* (F, GH, US).

PANAMA. **Bocas del Toro:** 15 km S of Changuinola, trail along river upstream from Changuinola 1-dam site, ca 900 ft, 13 Dec 1979 (fr), *Antonio 3169* (MO); Bocas del Toro, 6 Nov 1920 (fl), *Carleton 67* (GH, US); Al N.O. del campamento Changuinola 1 de

Corriente Grande, Cerro Bracha, 18 Jan 1980 (fl), *Correa et al. 3228* (MO); Changuinola to 5 miles S at junction of Ríos Changuinola and Terebe, 100-200 ft, 17-19 Dec 1966 (fl), *Lewis et al 842* (MO); Isla San Cristobal, Bocatorito, 30 m, 3 Feb 1989 (fl, fr), *Peterson & Annable 6564* (US); Isla Colón, 0-120 m, 20 Aug 1940 (fl), *von Wedel 493* (GH). **Canal Zone:** Near Summit Naval Radio Station, 19 Dec 1970 (fl), *Croat 12855* (F); Cocoli, parking area near stream, 4 Apr 1970 (st) *D'Arcy 3941* (MO); Junction of C-2 road with Gallard Highway, 11 Feb 1973 (fr) *Kennedy 2370* (US); Chivi-Chivi trail, 2 miles above Red Tank, 28 May 1923 (fr), *Maxon & Harvey 6584* (GH, US); Roadside at Portobelo-Puerto Pilon road at bridge over Rio Guanche, 5 m, 22 Sep 1973 (fl, fr), *Nee 7086* (MO); Las Cascadas Plantation, near Summit, 2 Dec 1923 (fl), *Standley 25803* (US). **Chiriquí:** 1 mi west of airport at Puerto Armuelles, near sea level, 17 Feb 1973 (fl), *Croat 21907* (BM, F, US); Near Rio San Juan, 19 Apr 1970 (fl), *D'Arcy 4291* (MO); Boquete, Cerro Horqueta, 5000-6000 ft, 8 Aug 1967 (fl), *Dwyer & Hayden 7760* (MO); Border of Chiriquí and Bocas del Toro, along continental divide on trail in Zona Protectora Palo Seco, 8°47'N, 82°13'W, 1100-1300 m, 11 Aug 2000 (fr), *Knapp & Mallet 9192* (BM). **Coclé:** Near village of Quebrada El Hato, turnoff 7 km W of Aguadulce on Pan-American Highway, 8°13'N, 80°40'W, 10 m, 12 Feb 1982 (fl), *Knapp & Clary 3374* (MO); Between Las Margaritas and El Valle, 15 Jul-8 Aug 1938 (fl, fr), *Woodson et al. 1770* (A, F). **Colón:** Along Río Iguanita, ca 3 km above the bridge on Portobelo Road, 9°27'N, 79°40'W, less than 100 m, 4 Apr 1980 (fr), *Croat 49755* (MO); Above Paseo la Canoa, 2100 ft, 11 May 1971 (fl), *D'Arcy 5434* (MO); Chagres, Isthmus of Panama, Feb-Mar 1850 (fl), *Fendler 253* (BM, G, GH, K, US, W); 2-4 km up the Río Guanche from the Portobelo Highway, 9°30'N, 79°40'W, 0-50 m, 3 Oct 1981 (fl), *Knapp 1426* (MO); 1-2 km from the Portobelo Highway up the Río Guanche, 9°30'N, 79°40'W,

0-50 m, 17 Feb 1982 (fl), *Knapp & Schmalzel 3581* (MO). **Darien:** Along Río Chico and in floodplain from Nazareht to approx. 10 km upstream, 8°15'N, 77°35'W, 100 m, 22 Dec 1980 (fl), *Hahn 185* (MO); Rio Balsas just above Rio Coasi, 2 Jan 1981 (fl), *Hartman 12512* (MO). **Herrera:** 50 metros de la carretera de Portobelillo, cerca de Chitré, 19 Nov 1971 (fl), *Salazar 28* (F). **Los Santos:** 3 miles S of Carreta, ca 5 miles S of Las Tablas, 24 Dec 1966 (fl), *Burch et al. 1247* (K, US); Entrada a el camino a La Lajita, El Guásimo de Los Santos, 1 Dec 1986 (fl), *Rodriguez 71* (F, MO). **Panamá:** Chepo, 11 Nov 1973 (fl), *Chávez 46* (F); South of Tocumen airport, 15 Nov 1975 (fl), *D'Arcy 9642* (MO); Monte situado atrás del Auto Cine Olímpico, 7 Oct 1974 (fl), *Him 35* (F); Interior of Isla Salaga, Perlas Islands, 8°38'N, 79°05'W, 0-100 m, 29 Jan 1982 (fl, fr), *Knapp 3278* (MO); Tocumen Marsh, SE of Aeropuerto Omer Torrijos H., 9°05'N, 78°27'W, 0 m, 3 May 1982 (fl), *Knapp 4937* (MO); 6 km S of Arraijan, 10 m, 28 Aug 1973 (fl, fr), *Nee 6646* (MO); Chepo, about 60 m, Oct 1911 (fl), *Pittier 4449* (US); Golfo de Panama, Isla Taboga, 18 Apr 1972 (fl), *Plowman 3162* (K, US); Base of Serranía de Cañazas, ca. 15 km SW of Cañaza near Río Torti, 8°52'N, 78°22'W, 150 m, 15 Jan 1983 (fl), *Stein 1373* (MO). **San Jose Island:** Pearl Archipelago, near Main Beach, 30 Apr 1945 (fl, fr), *Erlanson 6* (US); Near Punta del Cabo, San José Island, 8°14-15'N, 79°08-09'W, 18 Aug 1945 (fl), *Harlow 18* (US); Perlas archipelago, Gulf of Panama, about 55 miles SSE of Balboa, Naval Station, 30 Oct 1944 (fl), *Johnston 328* (BM, GH). **Veraguas:** Trail between Cañazas and the foot of the Cordillera Central, headwaters of Río Cañazas, 300-600 m, 8 Feb 1937 (fr), *Allen 156* (F, MO); Bahia Honda, 28 Mar 1939 (fl), *Elmore H8* (F, US).

WEST INDIES: **Tobago:** At Great Dry River, Nov 1889 (fl), *Eggers 5796* (US); Forest Reservoir, 1 Feb 1953 (fl), *Hunnewell 19987* (GH); Roxborough-Bloody Bay

road, 700 ft, 12 Aug 1958 (fl), *Purseglove P.6345* (K, US). **Trinidad:** Penal Rock Road, 28 Mar 1920 (fl, fr), *Britton et al. 1075* (US); Moruga, 19 Mar 1921 (fr), *Britton & Broadway 2447* (GH, US); Woodbrook, 31 Oct 1923 (fl, fr), *Broadway 5191* (G, GH, MO).

VENEZUELA. **Aragua:** 1 km N of Ocumare de la Costa, on rd. to Cata (seed collected in Venezuela and cultivated at Cornell), 19 Jun 1982 (fl), *Caruso s.n.* (F); Maracay, 1928 (fl, fr), *Vogel 847* (M). **Barinas:** Dist. Pedraza, secondary road from Curbatí to El Algarrobo, ca. 55 km SW of Barinas, 8°31' N, 70°35' W, 200-360 m, 15 Nov 1990 (fl), *Dorr & Barnett 7723* (US). **Bolívar:** El Dorado, 30 Apr 1957 (fr), *Couret 211* (US). **Carabobo:** La Cumaca, near San Diego, 500 m, 31 Dec 1938 (fl), *Alston 5887* (BM, US). **Choco:** Río Truando, gallery between the boom (bun) and Río Salado, 18 May 1967 (fl), *Duke 11102* (US). **Cordoba:** Monteria, orillas del Río Sinú, hacienda El Covao, 140 m, 28 May 1950 (fl), *Garcia-Barriga 13423* (US). **Delta Amacuro:** Este de Río Grande, este-noreste de El Palmar, cerca de los límites del Estado Bolívar, 12 Jan 1964 (fl), *Berti 549* (F); Between La Margarita and Puerto Miranda, Rio Acure, 80-100 m, 23-24 Nov 1960 (fl, fr), *Steyermark 87711* (K, US). **Falcón:** Near Santa Rosa, Lara, 4 Jan 1929 (fl), *Pittier 13091* (US); Parque Nacional Quebrada de la Cueva El Toro, 10°50'N, 69°07'W, 600 m, 21 Jun 1979 (fl), *Liesner et al. 7769* (MO). **Guárico:** Baños de San Juan de los Morros, Aragua, 8 Apr 1927 (fl), *Pittier 12307* (G, M, US). **Miranda:** Santa Lucía, 150-200 m, 6-8 Mar 1943 (fl, fr), *Killip & Tamayo 37003* (F, US); 2 km S of Río Chico along carretera 11, 28 Apr 1971 (fl), *Nee & Mori 4077* (US). **Monagas:** Caripito, 30 Mar 1940 (fl), *Pittier 14368* (US). **Sucre:** Península de París, 10°41'N, 63°22'W, 300 m, 14 Jul 1997 (fr), *Silva 1318* (M). **Tachira:**Dist. Jáuregui, Mun. J. T. Colmenares, parcela 58 de la Unidad Agropecuaria de Los Andes, Morotuto, 120 m, 3

Sep 1967 (fl, fr), *Steyermark & Velasco 100050* (US). **Trujillo:** Hacienda Carmona, 27 Aug 1941 (fl), *Tamayo 1807* (US). **Yaracuy:** Río Taría, ¼ km downstream from carretera 1 bridge at Taría, 19 Apr 1971 (fl,fr), *Nee & Mori 3980* (US). **Zulia:** +/- 20 km N.W. of El Vigia, Caño Padre, 0-50 m, 2 Dec 1966 (fl), *de Bruijn 1329* (K).

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Appendix 1. Vouchers for Crossing Studies.

S. aturense. Vouchers: *Bohs 2976* (UT). Collected in Costa Rica, Puntarenas, Canton Parrita; *Bohs 2555* (UT). Collected in Costa Rica, Estrella, Casamata.

S. jamaicense. Voucher: *Bohs 2482* (UT). Collected in Costa Rica, La Selva.

S. leucopogon. Voucher: *Bohs 3648 (UT).* Collected in Ecuador, Orellana, Estacion Biologica Yasuni.

S. pedemontanum. Voucher: *Bohs 3643* (UT). Collected in Ecuador, Orellana, Estacion Biologica Yasuni.

S. tampicense. Voucher: *Bohs & Stern 3655* (UT). Collected in Florida, Highlands Co., Fisheating Creek.

S. volubile. Voucher: *Bohs 2473* (UT). Costa Rica, La Selva.

Numerical List of Species

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2. *S. arachnidanthum*
3. *S. asperrimum*
4. *S. aturense*
5. *S. flexicaule*
6. *S. jamaicense*
7. *S. lanceifolium*
8. *S. leucopogon*
9. *S. monachophyllum*
10. *S. pedemontanum*
11. *S. tampicense*
12. *S. volubile*

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Steyermark & Liesner 118257 (3)

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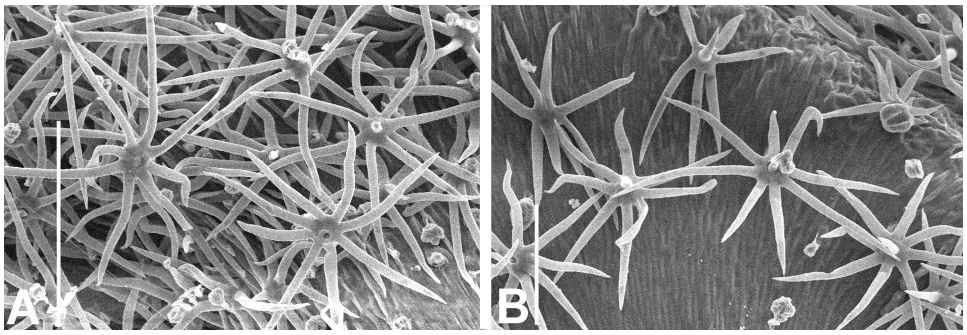

Fig. 1. Representative hairs of section *Eriophyllum* (*S. pedemontanum, Bohs 3643*, greenhouse grown UT). A. Dense stem pubescence, note the reduced midpoints. B. Moderate pubescence at the base of a prickle, note that the hairs are nearly sessile due to a reduced stalk. Scale bars. A = 400 μm, B = 200 μm.

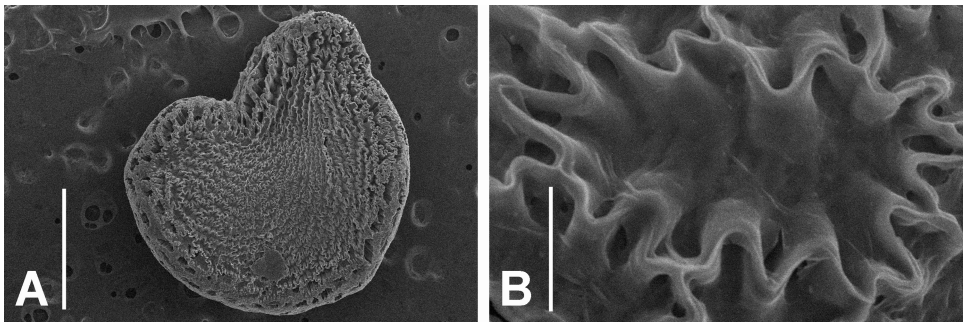

Fig. 2. Representative seeds of section *Eriophyllum* (*S. tampicense, Bohs & Stern 3655*, UT). A. Overview of enzymatically digested seed showing the minute pitting. B. Cell wall of a single seed cell with "amoeboid" invaginations of cell wall. Scale bars. A = 1 mm, B = 50 μm

Fig. 3. Flowers of *S. pedemontanum* with two stamens removed to reveal style (*Bohs 3643*, greenhouse grown UT). A. Functionally perfect flower, note long style that is exserted beyond the stamens. B. Functionally male flower, note the reduced style length and unexpanded stigma. Scale bars All = 1 cm.

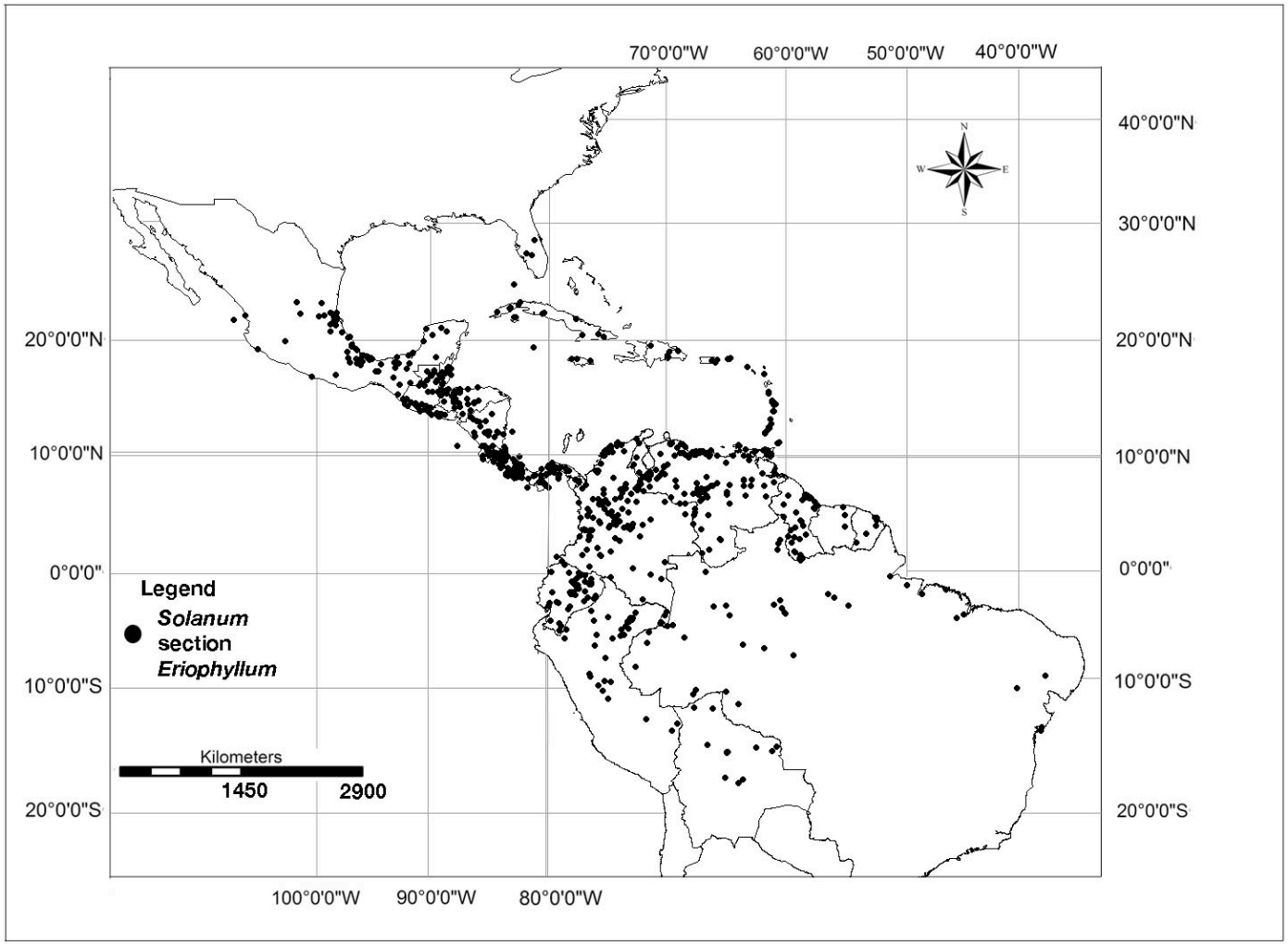

Fig. 4. Distribution of *Solanum* sect. *Eriophyllum*.

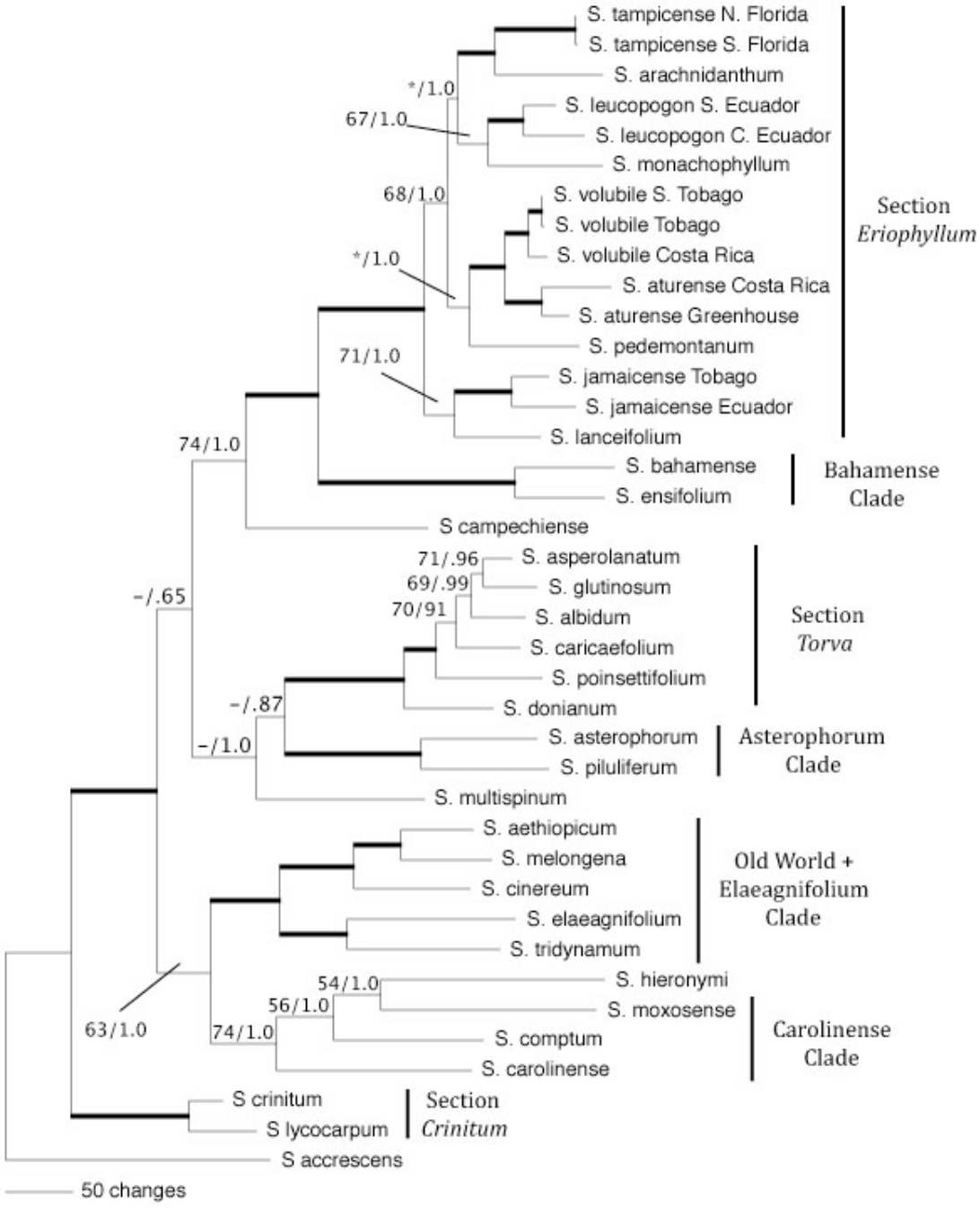

Fig. 5. One of the two most parsimonious trees recovered from the concatenated MP analysis of Stern and Bohs (in prep.). Bootstrap and posterior probabilities are shown above the branches. Thickened branches indicate nodes with > 90% BS and 0.95 PP. Asterisks indicate the nodes that collapse in the MP strict consensus tree and dashes indicate BS values below 50%. Formally named sections are labeled while major clades lacking formal names are indicated following Levin et al. (2006) and Stern et al. (2011).

Fig. 6. Scan of the holotype of *S. apaporanum*.

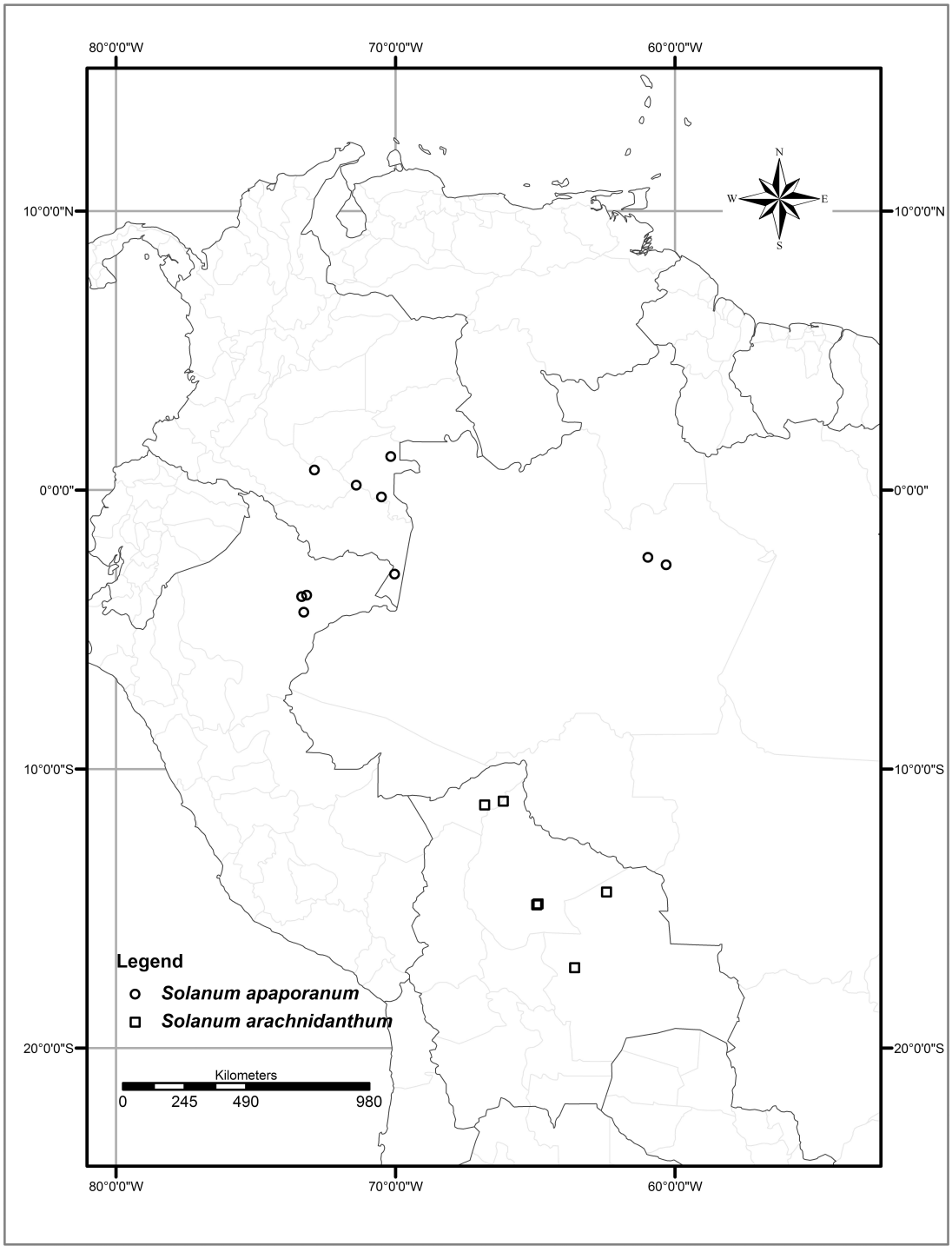

Fig. 7. Distribution of *S. apaporanum* and *S. arachnidanthum*.

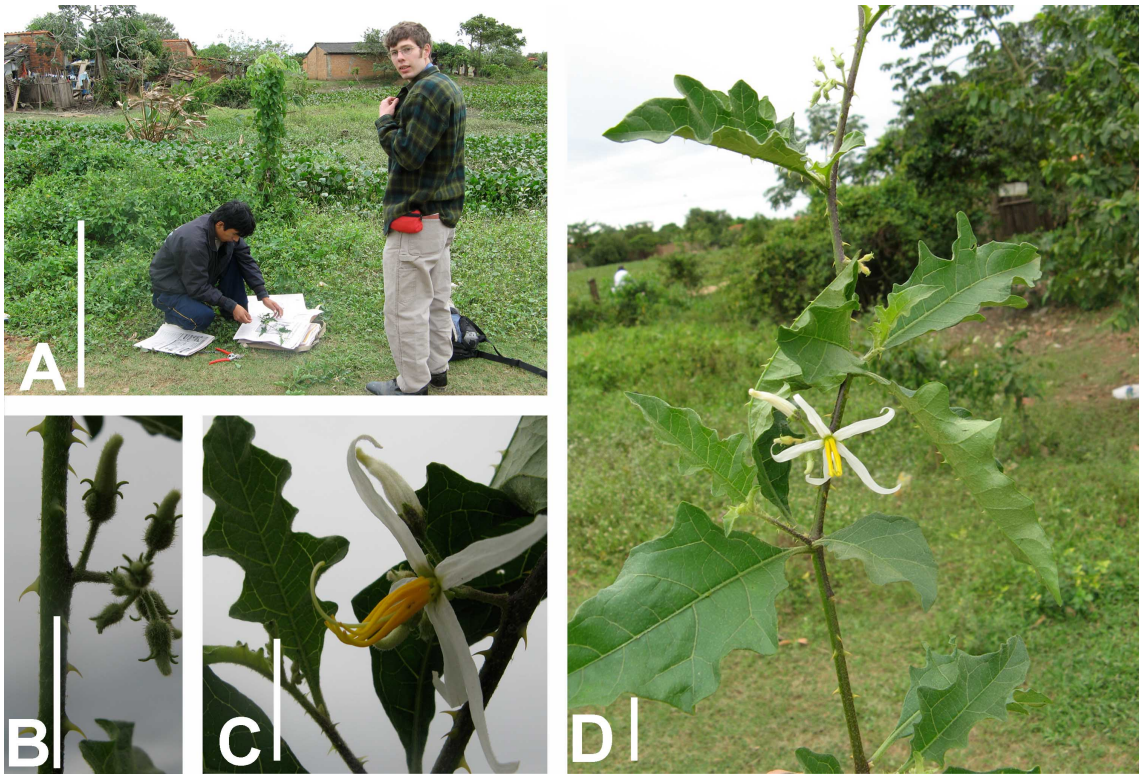

Fig. 8. Habitat and morphology of *S. arachnidanthum*. A. Habitat and habit in Trinidad, Boliva (*D. McClelland, A. Molina, & S. Stern 412*, NY). B. Stem and buds, note recurved calyx lobes and spines and stellate hairs. C. Mature flowers and lobed leaves. D. Habit and sympodial growth, note the difoliate sympodial units. Scale bars. A = 1 m, B, C, D = 2 cm.

Fig. 9. Scan of the holotype of *S. asperrimum*.

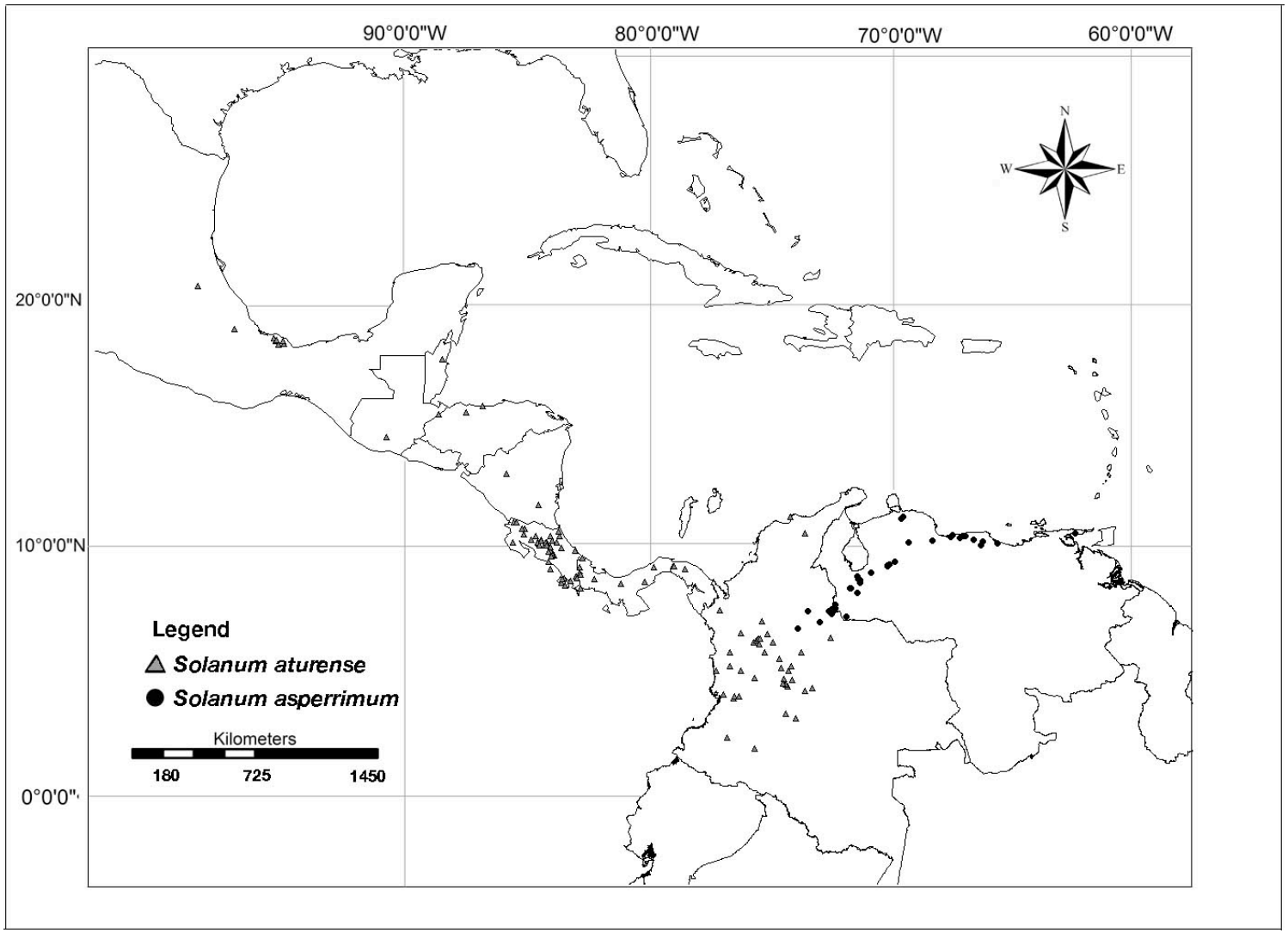

Fig. 10. Distribution of *S. asperrimum* and *S. aturense*.

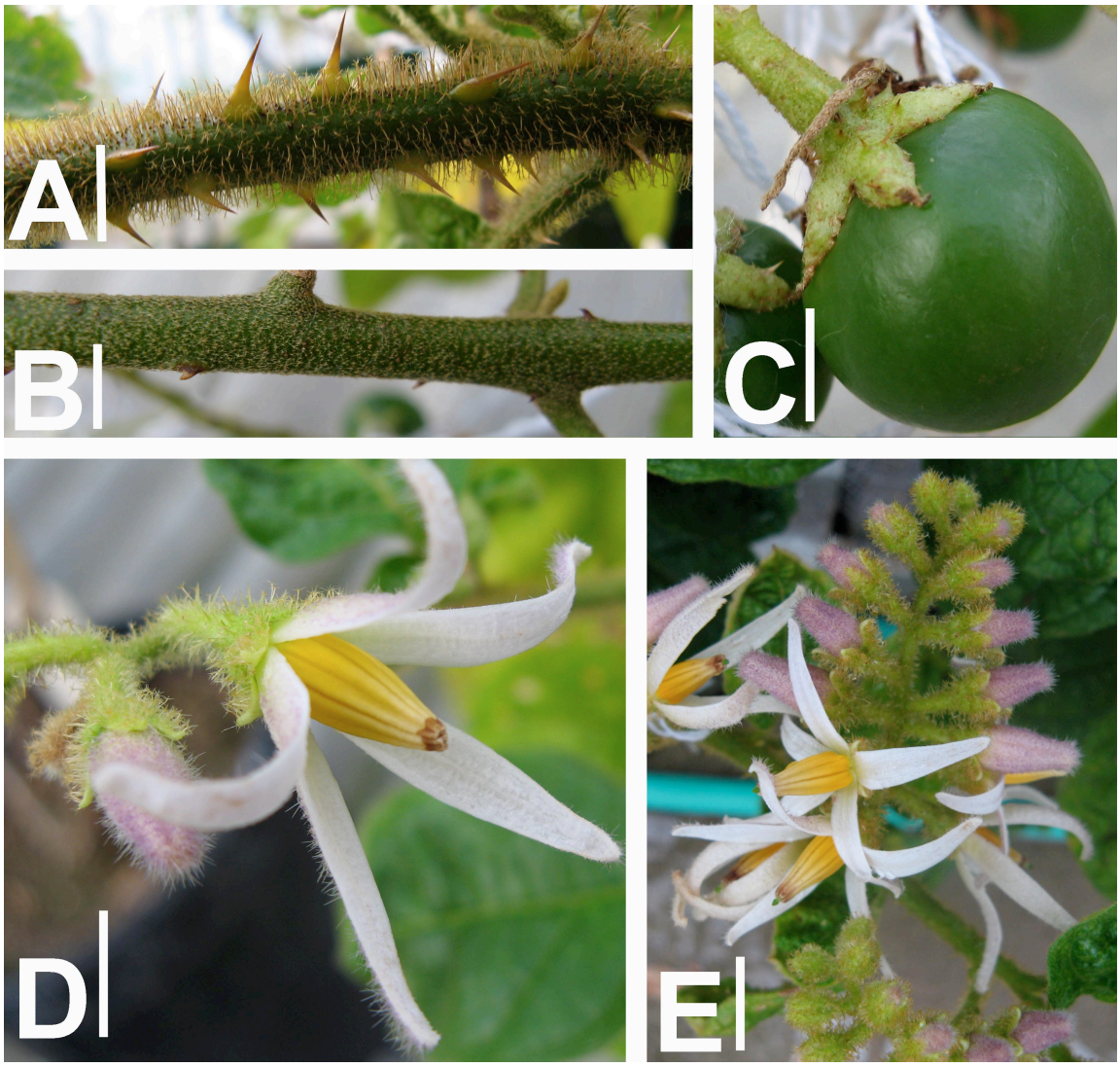

Fig. 11. Morphology of *S. aturense*. A. Spines and bristle-like pubescence. B. Stem with greatly reduced stalks on the stellate hairs. C. Immature fruit, note prickles on calyx. D. Flower. E. Inflorescence, note the purple tinge of the young buds. Scale bar. A, B = 3 mm. C, D, E = 1 cm.

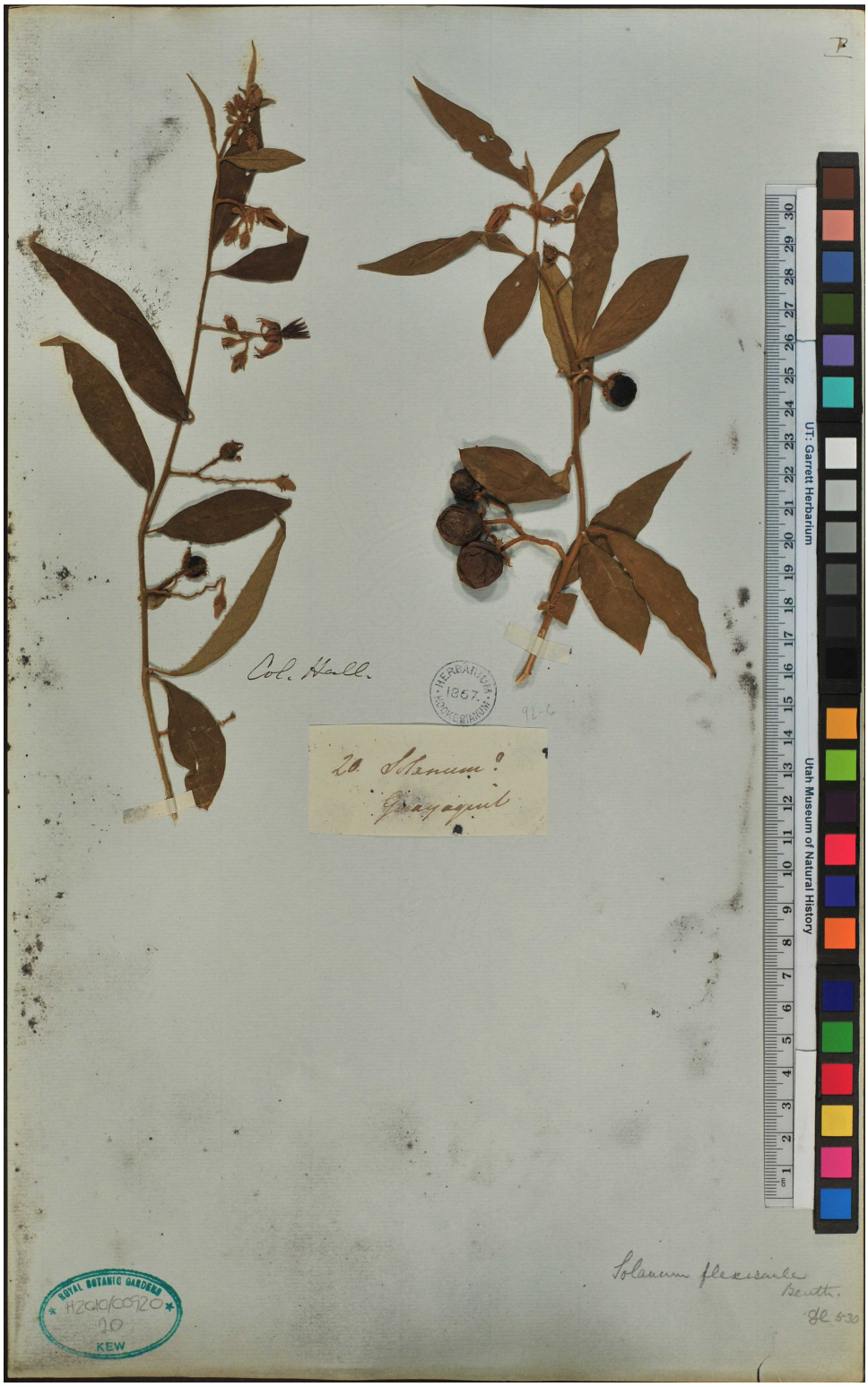

Fig. 12. Scan of a representative specimen of *S. flexicaule*.

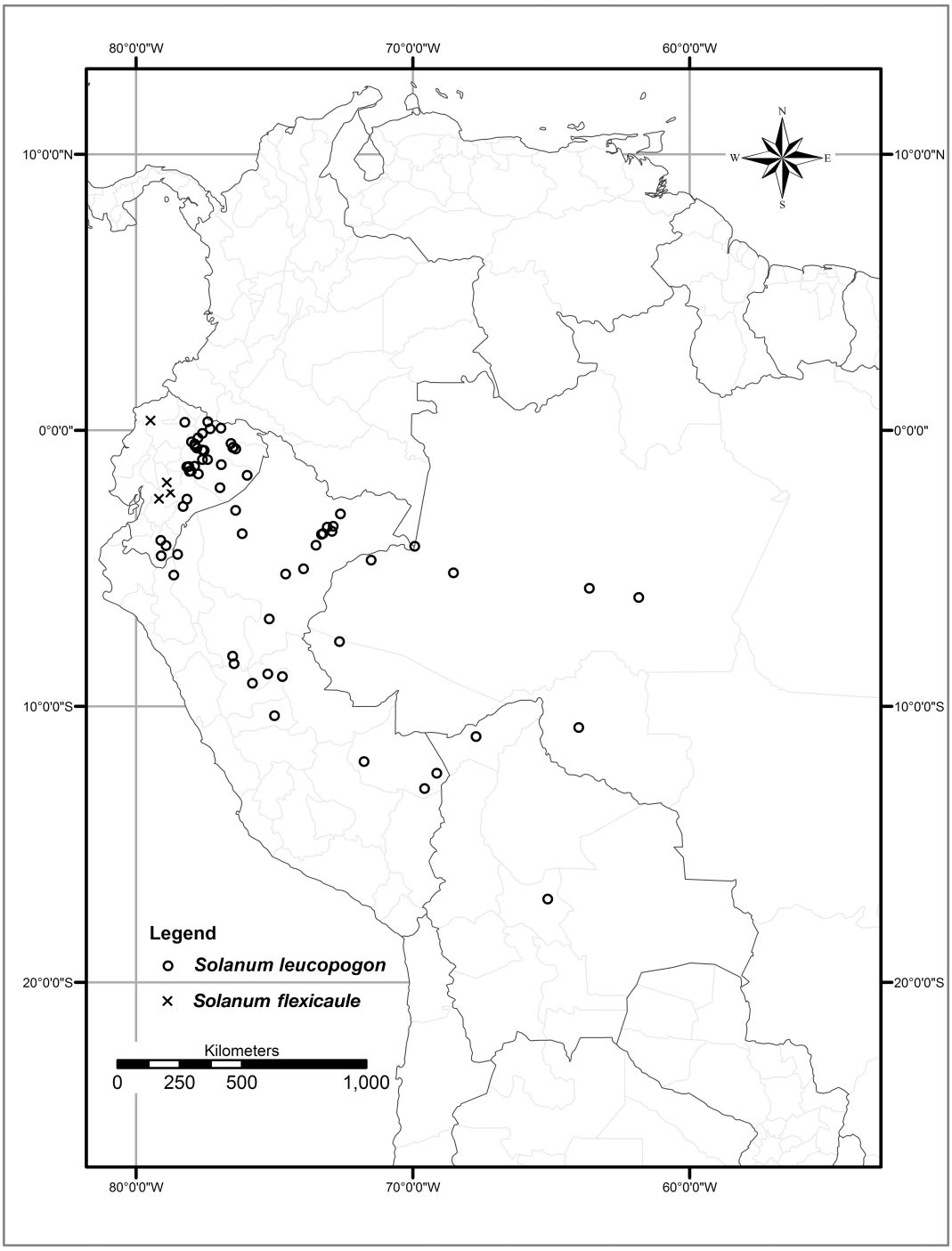

Fig. 13. Distribution of *S. flexicaule* and *S. leucopogon*.

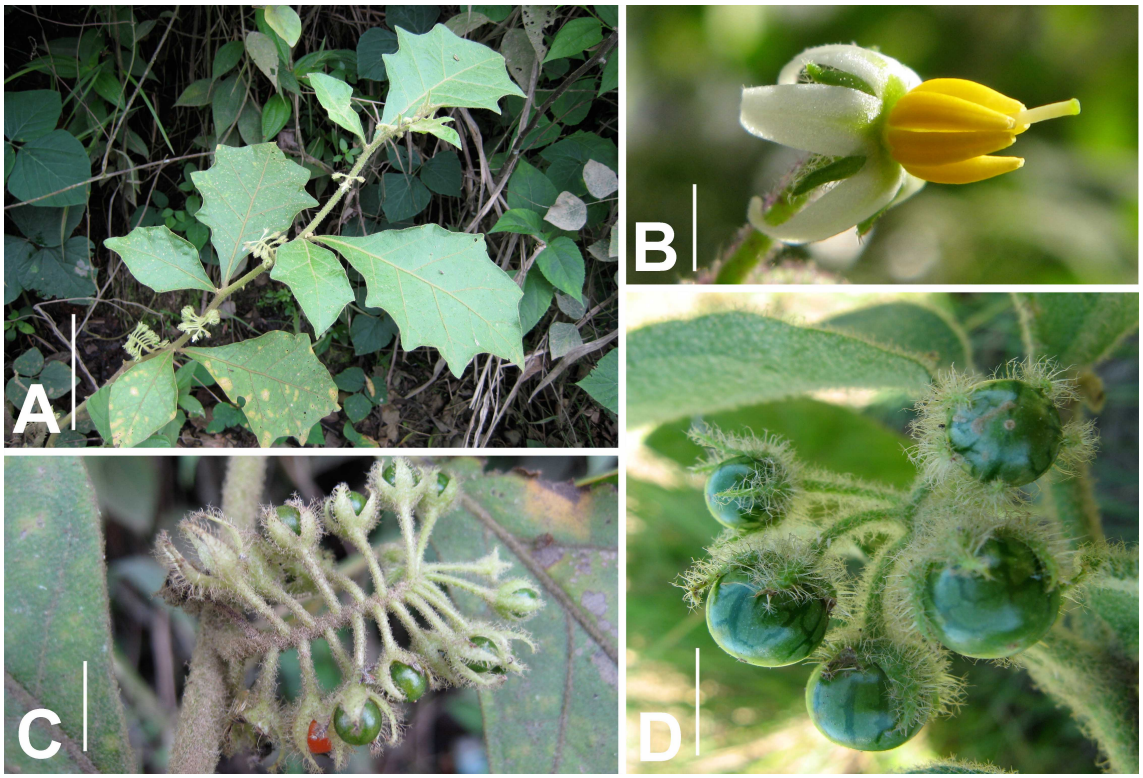

Fig. 14. Habit and morphology of *S. jamaicense*. A. Habit and leaf morphology, note the decurrent leaf base (*Stern & Tepe 389,* UT). B. Flower, note the recurved petals and the slightly off-centered style (B-C *Bohs 2482*, greenhouse grown UT). C. Inflorescence. D. Immature fruits, note mottling (*Stern 32*, UT). Scale bars. A = 8 cm, B = 5 mm, C, D = 1 cm.

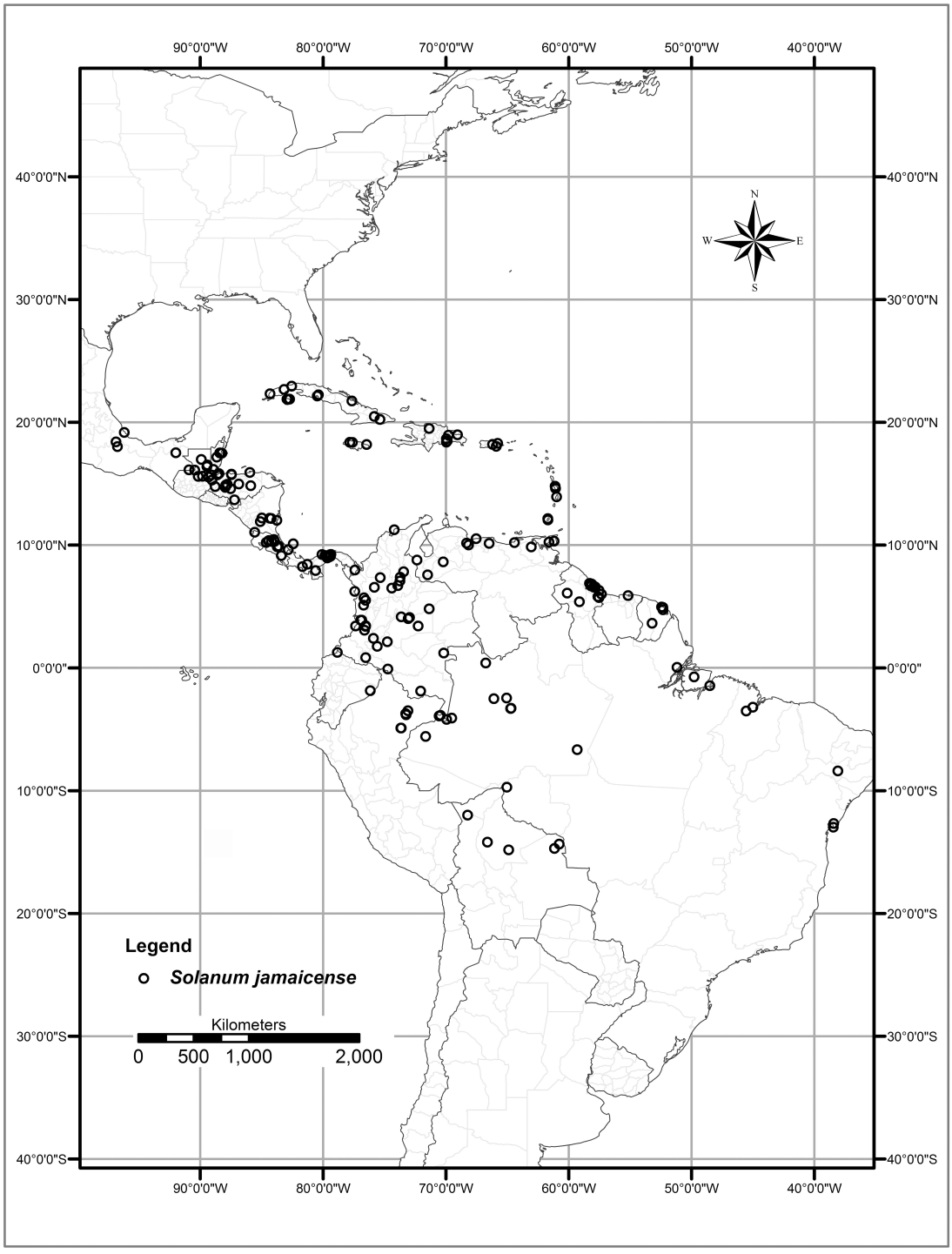

Fig. 15. Distribution of *S. jamaicense*.

Fig. 16. Scan of a representative specimen of *S. lanceifolium*.

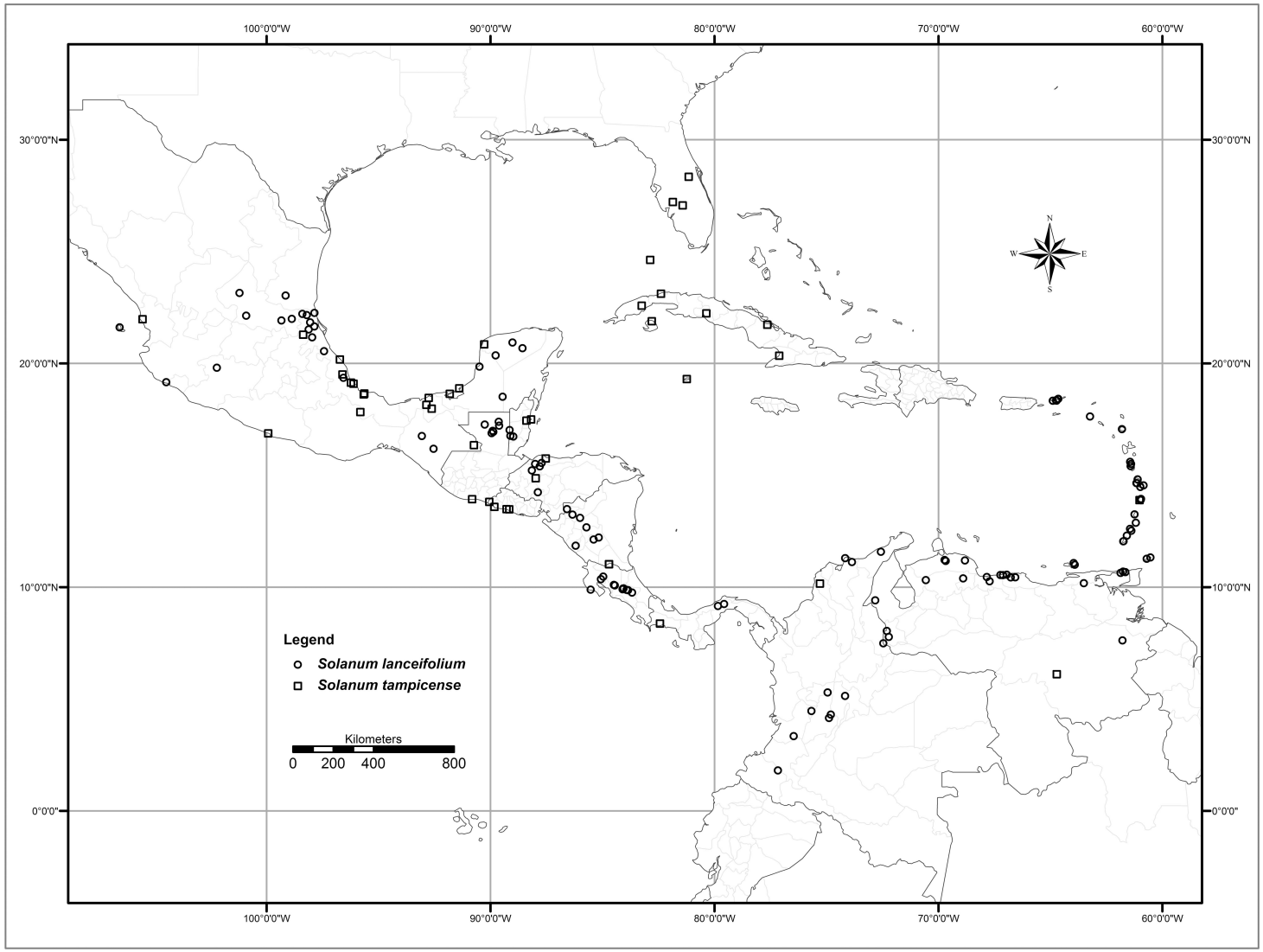

Fig 17. Distribution of *S. lanceifolium* and *S. tampicense*

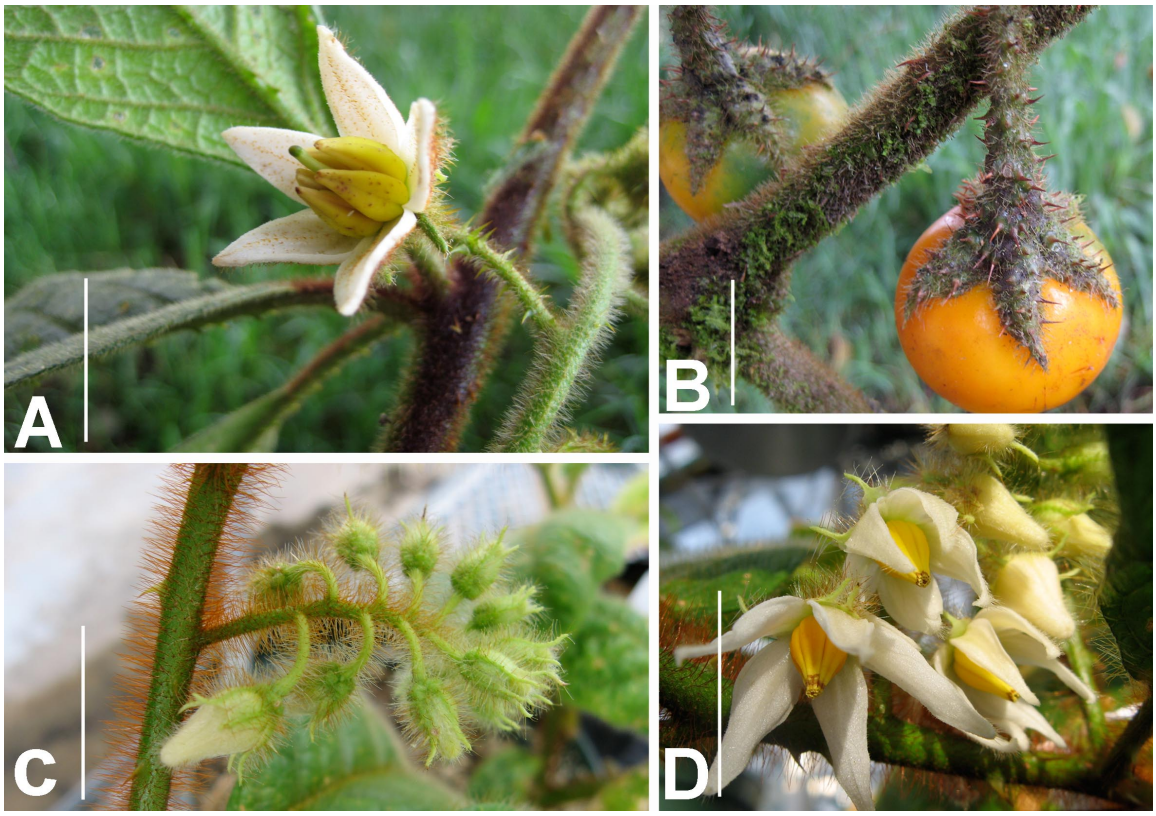

Fig. 18. Morphology of *S. leucopogon*. A. Hermaphroditic flower, note the style exserted beyond stamens (A, B = *Stern & Tepe 271*, UT). B. Mature fruits, note spines on calyx. C. Stem and inflorescence, note the long, red stem hairs and thin calyx lobes. D. Inflorescence of functionally male flowers, note that the styles are not exserted beyond the stamens. (C, D = *Bohs 3648*, greenhouse grown UT)

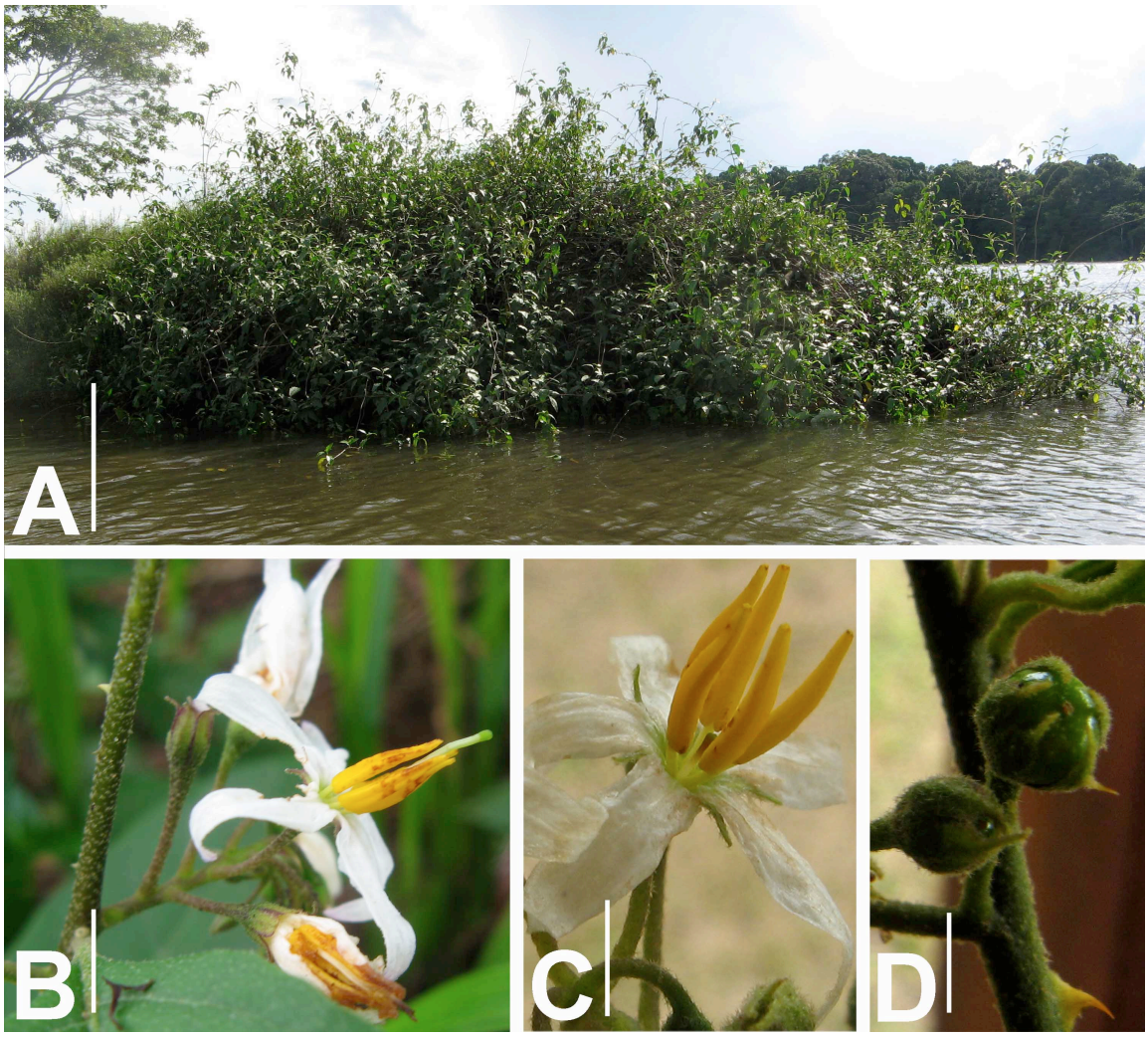

Fig. 19. Habit and morphology of *S. monachophyllum*. A. Habit of *S. monachophyllum* on a sandbar in the Essequibo River, Guyana. The high water marks were 3 m above the rootstock of this individual (*Stern 256*, UT). B. Inflorescence, note the elongate style and the damage to anthers done by bee pollinators (B-D *Stern 252,* UT). C. Male flower, note the reduced style. D. Young fruits and spines. Scale bars. A= 1 m, B, C, D = 5 mm.

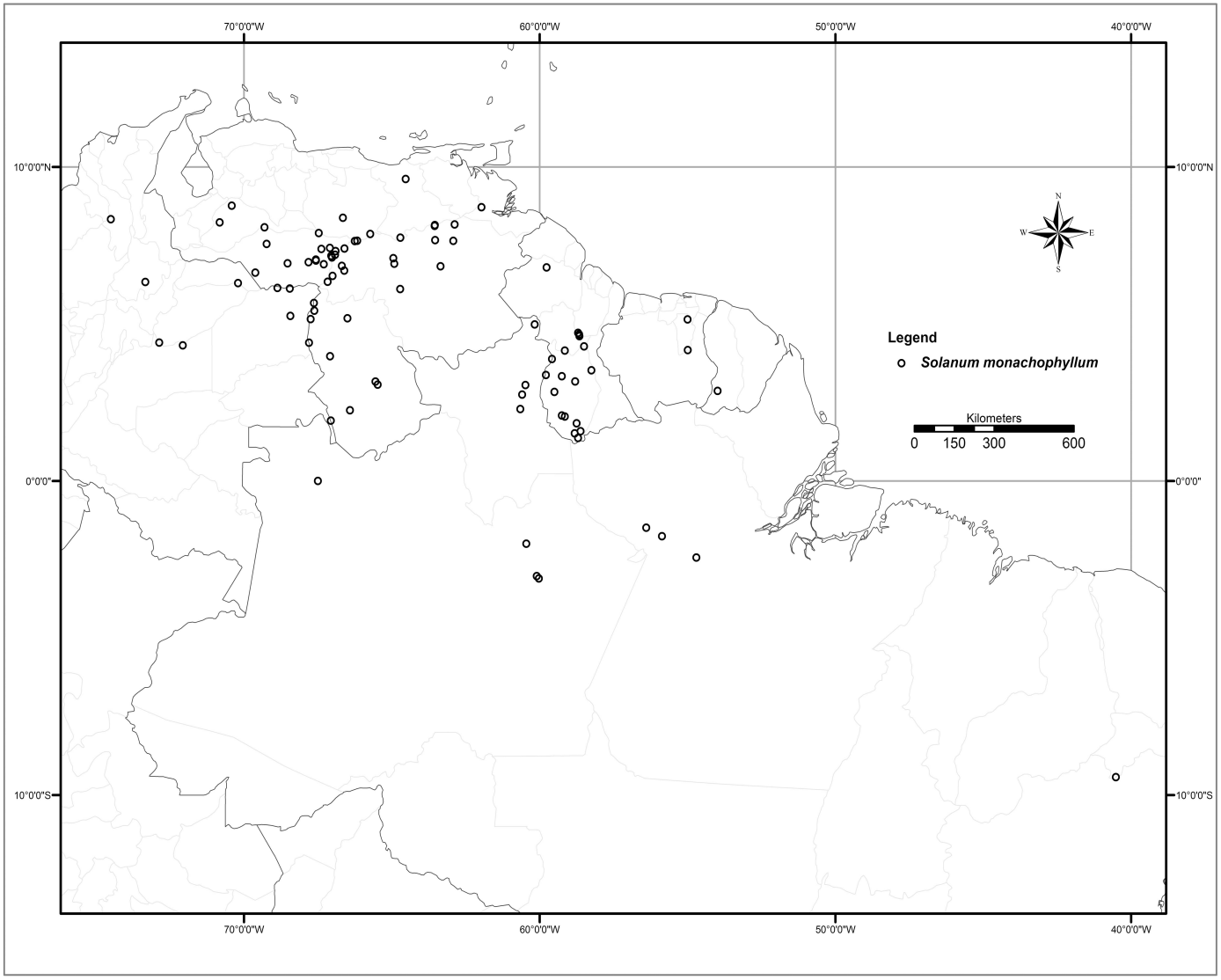

Fig 20. Distribution of *S. monachophyllum*.

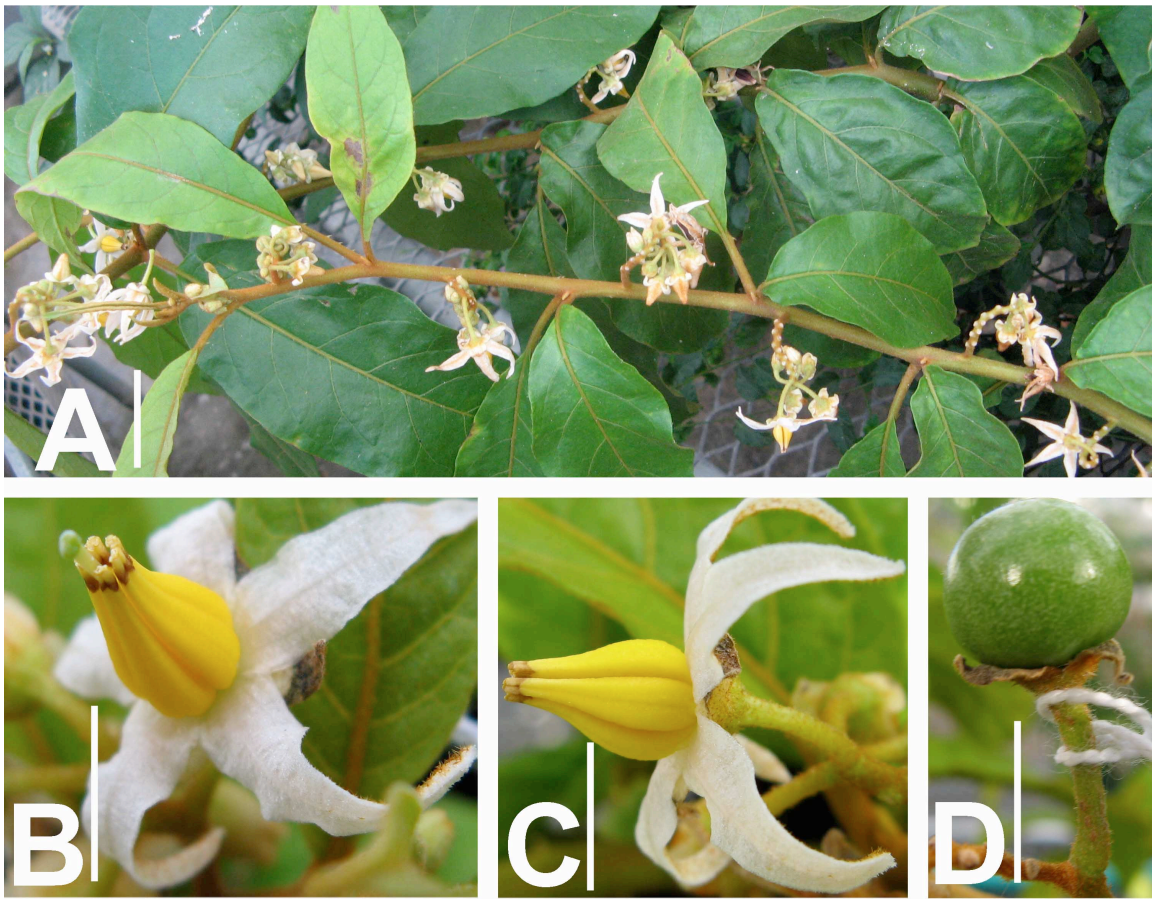

Fig. 21. Habit and morphology of *S. pedemontanum*. A. Habit, note the difoliate sympodial units (A, B, C, D = *Bohs 3643*, greenhouse grown UT) B. Hermaphroditic flower, note the style exerted beyond the stamens. C. Male flower, note the style is not visible. D. Immature fruit. Scale bars. A = 3 cm, B,C,D = 1 cm.

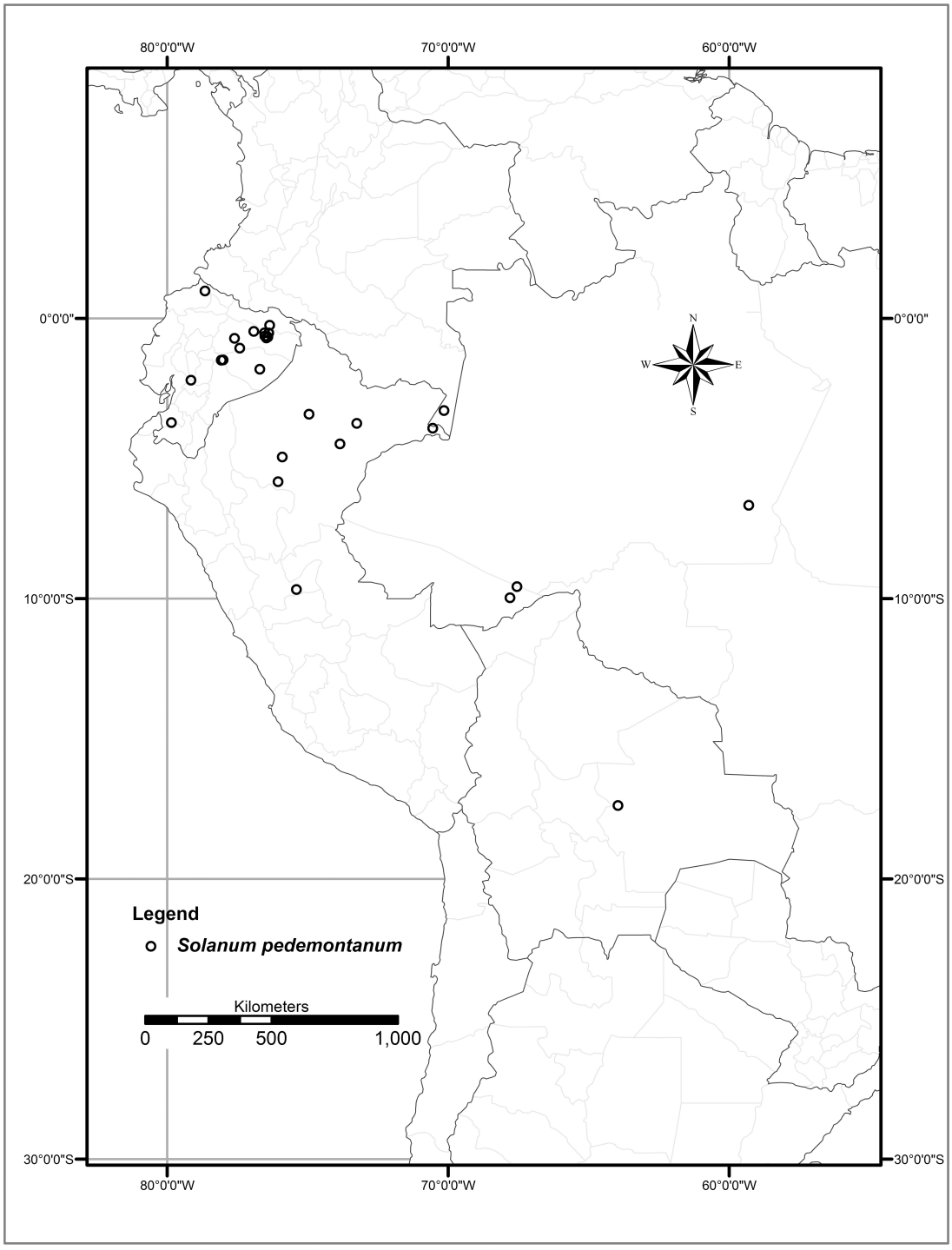

Fig. 22. Distribution of *S. pedemontanum*.

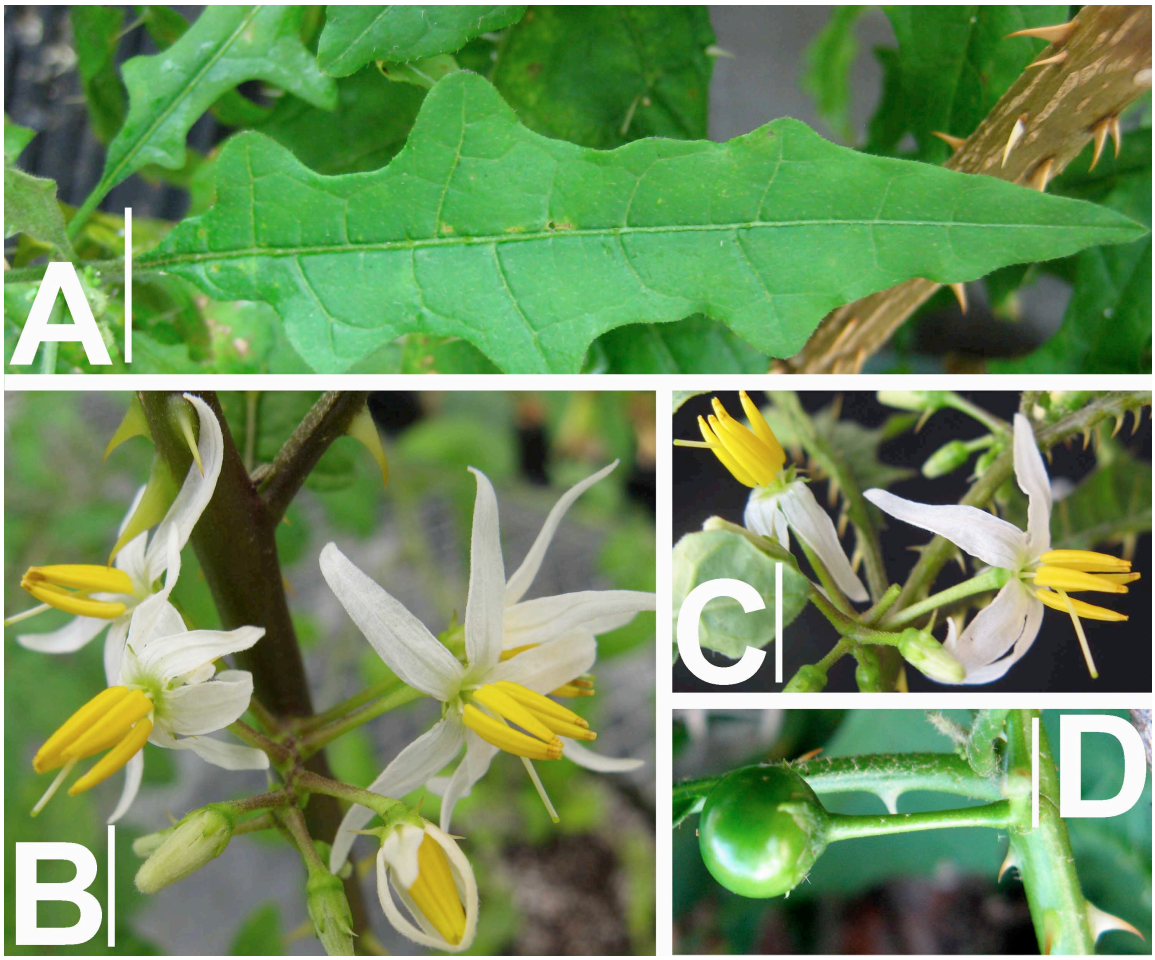

Fig. 23. Morphology of *S. tampicense*. A. Lobed leaf and recurved spines on stem (A, B, C, D = *Bohs & Stern 3655*, UT). B. Inflorescence, note the nearly glabrous stem. C. Flowers with off-centered style. D. Immature fruit, note the lack of peduncle. Scale bars. A = 1 cm. B,C,D = 5 mm.

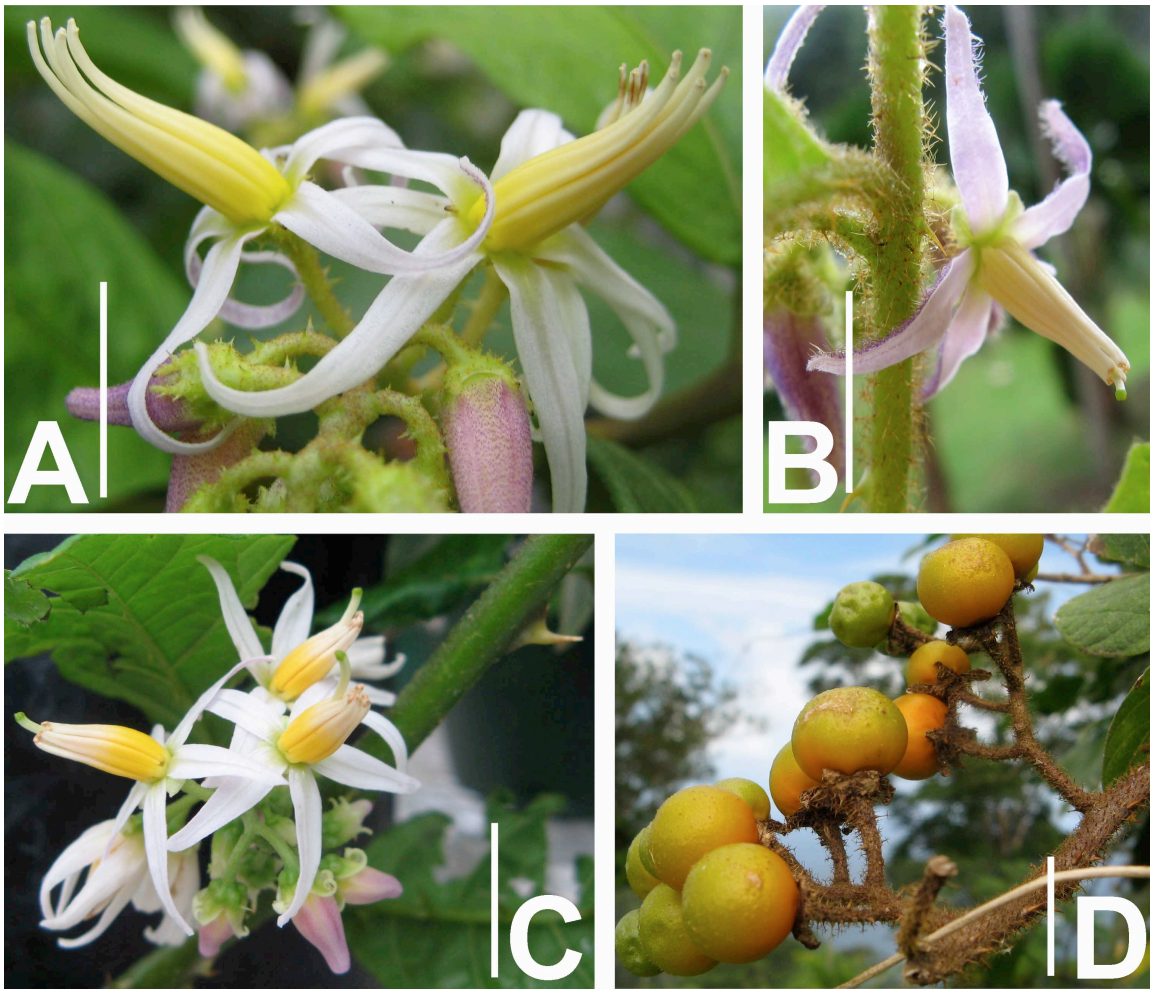

Fig. 24. Morphology of *S. volubile*. A. Functionally male flowers, note the style is not exserted beyond stamens (A, B, D = *Stern 263*, UT). B. Hermaphroditic flower, note the style exserted beyond stamens and the bristle-like pubescence. C. Greenhouse grown plant, note spine and the nearly glabrous stem (C = *Bohs 2473*, greenhouse grown UT). D. Mature fruits. Scale bars. A, B, C, D = 1 cm.

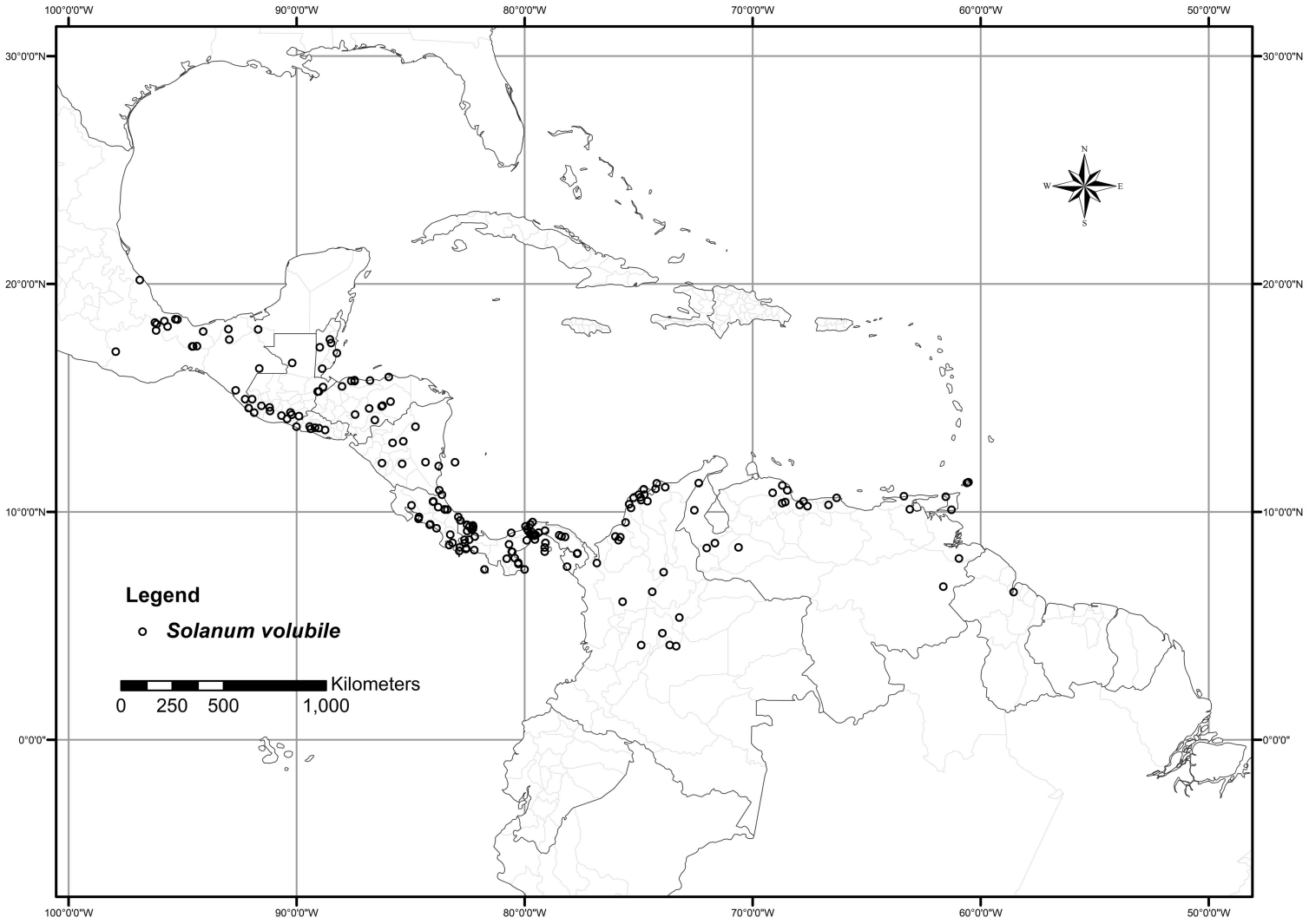

Fig. 25. Distribution of *S. volubile*.